DIFFERENTIAL HABITAT UTILIZATION OF FOUR AFRICAN *CERCOPITHECIDAE*

by

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Tell me what you eat, and I will tell you what you are.

Brillat-Savarin - Physiologie du Gout

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by

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Four African cercopithecoids, *Papio cynocephalus*, *Cercopithecus aethiops*, *Cercopithecus mitis*, and *Colobus angolensis*, are found coexisting in a small coastal forest in Kenya. A six-month field study was conducted to investigate their differential utilization of their habitats. Four troops, one of each species, were studied in a site in which their ranges overlapped. The project focused on investigation of diet and space-use patterns. Fecal samples were collected and analyzed as a means of qualitatively supplementing the observed data. Interspecific associations were formed containing as many as three species, and interactions were usually peaceful or neutral. Most occurrences of interspecific aggression and grooming were between the *Cercopithecus mitis* and *C. aethiops* troops. Habitat partitioning was found to be

resource related and was accomplished through differential reliance on food sources as well as differential means of exploiting overlapping resources.

CHAPTER I

INTRODUCTION

The occurrence of sympatric associations of related taxa is often a puzzling phenomenon, particularly when little is known about the exact relationships and competitive advantages of the species involved. Current ecological studies suggest that the persistence of sympatric species in a particular habitat are, in part, determined by the ecological differences which exist between them. Sympatric populations have often been maintained through effective partitioning, or differential utilization, of the habitat.

Resource partitioning is most often the means by which species coexist, and there are numerous strategies by which it can occur. When niches overlap to a large extent, natural selection may favor a process of niche displacement involving change in habitat, food selection, morphology, physiology, or behavior of one or both species. Differences in closely related species are often accentuated, or diverge, in sympatry; this is known as character displacement. Convergence, or the lessening of differences, has also been seen to be selectively advantageous in some sympatric situations (Cody, '69; Odum, '71).

Most of the studies concerning coexistence have focused on the mechanisms and interpretation of resource partitioning. Resource partitioning can be achieved in a variety of ways. Species may be separated spatially; this can occur through horizontal separation or, in some habitats, vertical separation. If coexisting species coincide in their spatial distribution, they may be partitioning the resources in terms of eating different food items, differing proportions of items, or, even more subtly, seasonally overlapping resources. Partitioning may also be effective through differences in particle size, temporal differences in foraging, or behavioral differences in foraging activities (Barash, '73; Crook and Aldrich-Blake, '68; Kunz, '73; Sabater Pi and Jones, '67; Laerm, '74; Cameron, '71; Erlinge, '72; Cody, '68; Baker and Baker, '73; Stallcup, '68; Groves, '73; Flake, '73; Gartlan and Struhsaker, '72; Brown, '71; Schoener, '68a, '68b; Pulliam and Enders, '71).

Until recently, the bulk of primatological research has concentrated on aspects of social structure and organization in relation to behavior, and most statements concerning the environment in which primates were found have come mainly from incidental observations which grew out of a wider behavioral study. While current research trends have begun to focus on primate ecology and more attention is being paid to the means by which the primates have differentiated through adaptive responses to their habitats, it has been realized that sympatric populations occur among the primates and polyspecific associations and intertaxa relations are frequent. Such communities, as well as those which include closely related taxa, have been described as containing species of widely different locomotive and digestive adaptations. However, the actual relationships between species in associating groups have not come to be fully understood nor have the different types of associations themselves begun to fall into any discernible pattern (Bernstein, '67; Gautier and Gautier-Hion, '69; Gartlan and Struhsaker, '72; Klein and Klein, '73). Most often these associations appear to be pacific and noncompetitive. Among sympatric populations, which are seen as coexisting without competition, partitioning appears to be resource related and accomplished in many of the ways mentioned earlier (Bernstein, '67; Thorington, '67; Struhsaker, '67a; Gartlan and Brian, '68; Jones and Sabater Pi, '68, '71; Richard, '70; Gartlan and Struhsaker, '72; Groves, '73).

Discussing adaptations at the "environment" or "habitat" level is not sufficient; it is only at the level of the "niche," as a definition of a species' ecological environment, that meaningful information about the placement and interrelationship of the species in the natural system and community can be reached. Thus, while the basic facts about the ecology of primates are becoming more a subject of investigation, little has been done to detail the ecological niche differences between species nor is attention being paid to understanding which differences are significant.

It was felt by the investigator that associations and interactions among sympatric species can be indicative of areas of resource overlap or exclusion. This is the premise upon which the present investigation was conceived.

The Diani Beach forest, which contains four diurnal primate species in three different genera, was seen as a situation which had potential value for an investigation of primate resource partitioning.

The main investigative method was to focus on feeding behavior, specifically on diet. The reasons for this approach were that little is known of the natural diets of primates, feeding is a major activity among primates, and considerable time and energy is directed toward feeding behavior (Jones, '72).

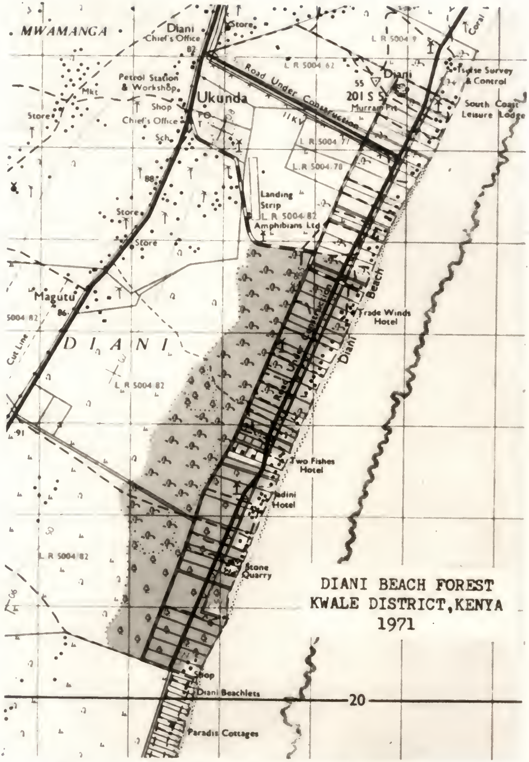
Since all behavior occurs in space and because resources are distributed in space, the space-use patterns of the species were also investigated. Finally, attention was also focused on the interrelationships and associations that occurred whenever any of the four species were in contact with one or more of the other species.

CHAPTER II

THE STUDY SITE

The field observations upon which the study is based were conducted in a small coastal forest in Kenya, East Africa, from October, 1972, through March, 1973 (fig. 1). The actual study site of the Diani Forest was a small section about 1100 m long, 150 to 200 m wide, and approximately 25 km south of Mombasa (fig. 2). Most of the following climatological and ecological description of the area is abstracted from Moomaw ('60), the Survey of Kenya ('62), and Greenhood ('71).

The coast of Kenya lies in the latitudes of the hot tropics extending from 1° 40' S to about 4° 40' S. The weather is largely affected and controlled by the monsoon air currents of the Indian Ocean. These currents, in combination with orographic effects of the coastal hills and convection over the hot, dry interior to the west, produce a marked bimodal distribution in the rainfall for most of the coast districts. The southeast monsoon brings the long rains in April, May, and June during which more than half of the annual precipitation usually falls; however, in the Mombasa area, the rains often end in July. The short rains usually occur in October and November



DIANI BEACH FOREST
KWALE DISTRICT,KENYA
1971

Fig. 1 Map of the Diani Beach forest

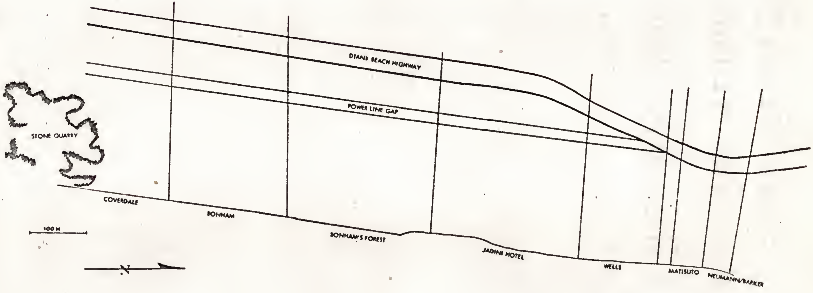


Fig. 2 Map of the study site in the Diani Beach forest.

(table 1). Information obtained from a local European citrus farmer (table 2) indicates a marked divergence from the recorded norm for the months of September and October. Rain showers occur mainly in the morning or midday hours. Rainfall varies between 76 to 102 cm, but occasionally goes higher. A total of 185 cm was recorded for 1972 by the same farmer mentioned above.

The forest occurs in the physiographical component 3 to 8 km. It generally lies below the 31-meter contour and displays a series of old, flat-bedded coral reefs and their associated lagoonal deposits of coral breccia, calcarious sands, and beach sands. The reef is backed by a series of variable sands which may be lagoonal, aeolian, or alluvial in origin. The area has a long history of settlement and cultivation which has a direct bearing on the distribution of the present vegetation.

Moomaw recognizes nine broad ecological or "land-use" units (table 3). These are distinguishable on the basis of vegetation, climate, and soils. The types are generally quite distinct and the boundaries (ecotones) between them apparent. The principle exceptions occur at the interfacing and invasion of the *Acacia-Euphorbia* of the interior with the *Manilkara-Diospyros* forest and the coppice and the savanna formation that takes place at the edge of the tropical rain forest types.

TABLE 1

Mean monthly precipitation for Mombasa (in cm)

	J	F	M	A	M	J	J	A	S	O	N	D
Moomaw	2.61	1.65	6.32	19.32	31.97	11.98	8.94	6.42	6.35	8.71	9.55	6.04
Survey of Kenya	2.54	1.90	6.75	19.68	33.65	11.43	9.52	6.35	6.35	8.25	9.52	5.91

TABLE 2

Monthly precipitation for Diani, 1972 - 1973 (in cm)

	J	F	M	A	M	J	J	A	S	O	N	D
European Citrus Farmer	9.49	N/A	N/A	N/A	N/A	N/A	N/A	N/A	14.47	34.95	6.17	5.63

N/A represents no information available.

TABLE 3

Major ecological land-use units (after Moomaw, '60)

Land-use unit	Description
I.	*Acacia-Euphorbia:* Acacia Thorn-bushland
II.	*Manilkara-Diospyros:* lowland dry forest: a) *Cynometra-Manilkara sulcata/Croton:* Sokoke forest b) *Manilkara-Dalbergia/Hyparrhenia:* shale soil savanna
III.	*Brachystegia-Afzelia:* lowland woodland
IV.	*Combretum schumannii-Cassipourea:* lowland dry forest on coral rag
V.	*Sterculia-Chlorophora/Memecylon:* lowland rain forest
VI.	*Albizia-Anona/Panicum:* lowland moist savanna
VII.	Sand beach and dune communities
VIII.	Mangrove swamps and saline margins
IX.	Pan and pond

The flora of the Diani Forest falls into category IV, *Combretum schumannii-Cassipourea:* lowland dry forest on coral rag. Moomaw sees the type IV forest as a distinct association which has been, for the most part, destroyed long ago. The soil fertility of type IV is relatively high, and it has been used for cultivation for many years, even where the coral outcrops are very near the surface. Maize, beans, cassava, and a wide variety of vegetable crops are produced, and the association furnishes the site for much of the coconut crop. Thus, the forest type presently occurs in isolated patches separated by cultivated plots and areas of secondary association. It does not extend appreciably north of Mida Creek and probably never exceeds 5 km in width. When the rainfall exceeds the 76 to 102 cm characteristic of type IV, the forest may take on the character of a rain forest; this may be the case for the Diani Forest.

Combretum schumannii and *Cassipourea euryoides* are present together and dominate, but one or the other may be the major species. *Fagara holtziana* and *F. chalybea* are striking members. Others present are: *Adansonia digitata, Mallotus oppositifolius, Rinorea sp., Hunteria africana, Erythroxylon emarginatum, Sideroxylon diospyroides,* and *Drypetes sp.*

The forest essentially consists of two layers: the upper canopy of tall, branching trees; and the under story frequently of *Pemphis acidula, Pycnocoma littoralis, Notobuxus obtusifolius,* and *Grewia vaughnii.* When the forest is destroyed, the characteristic coastal bush dominates; it is usually characterized by *Lantana camara, Commiphora sp., Combretum constrictum, Rhus natalensis, Securinega virosa, Hoslundia opposita, Grewia glandulos,* etc.

Moomaw further notes that two other retrogressive stages may be found. First, where fire follows cultivation and dense thicket formation, a savanna of *Hyparrhenia, Digitaria,* and *Heteropagon contortus,* and *Hyphaene compressa* develops. Second, when most of the shrubs and trees are destroyed, the doum palms (*Hyphaene compressa*) are left in a weedy grassland.

At the Diani locality, the forest remnant has undergone vast changes in the last five years. Significant amounts of the climax forest near the beach were destroyed between October, 1969, and June, 1970, through construction of transects for water mains and power lines. Clearing for a paved road was also begun at that time and completed just prior to the beginning of this project. This roadway (fig. 3) was estimated to be 10 km long running from the South Coast Leisure Lodge south to 4° 20' South Cottages (indicated as "Shop" in fig. 1). There were approximately

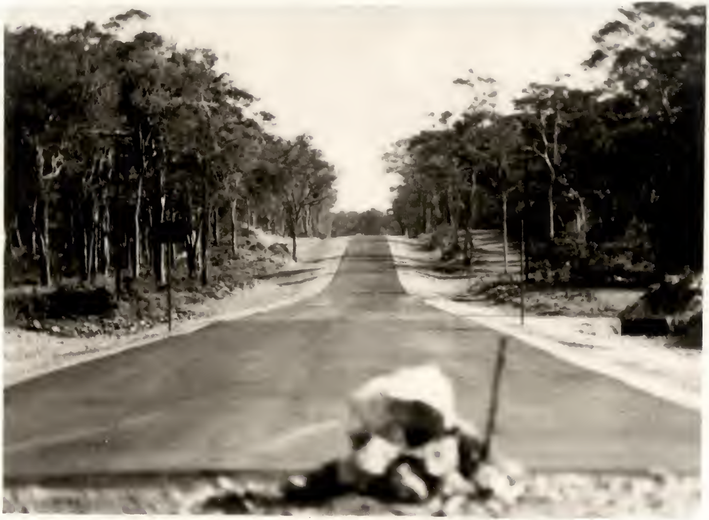


Fig. 3 The Diani Beach highway and the power lines recently constructed through the stand of primary forest at Diani Beach.

six meters of paved carriageway with a one-meter shoulder on each side to the drainage area. The area beyond the drainage was cleared in varying amounts so that the total cleared area was about 30 m on the average. The condition of the forest further deteriorated during the course of the project due to sporadic clearings within the forest for firewood and the construction of a large hotel complex (figs. 4 and 5). Although much of the forested coastal area is listed as protected, deforestation continues.

The forest supported a varied fauna. Present were: the long-nosed elephant shrew (*Rhynchocyox*), black-lipped mongoose (*Herpesles sp.*), bush pig (*Potamochoreus porcus*), bushbuck (*Tragelaphus scuptus*), red dukier (*Cephalophus natalensis*), suni (*Nesotraynes mochatus*), and dik dik (*Rhynchotrayus guentheri*). Lions were rare, but leopards occurred where there was sufficient cover. Nile monitors (*Varanus niloticus*) were common; Egyptian cobras (*Naya haje*), green mombas (*Dendroaspes angusticeps*), as well as several varieties of nonvenomous snakes were also present. The hawk eagle (*Hieraalus spilogastic*) was in the area, as were Kenya crested guinea fowl (*Grittera pucherani*) and hornbills (*Bucerotidae*).

The faunal assemblage included two species of galago: thick-tailed galagos (*Galago crassicaudatus*) and lesser galagos (*Galago senegalensis*). Also included were the four diurnal cercopithecoid species investigated in this

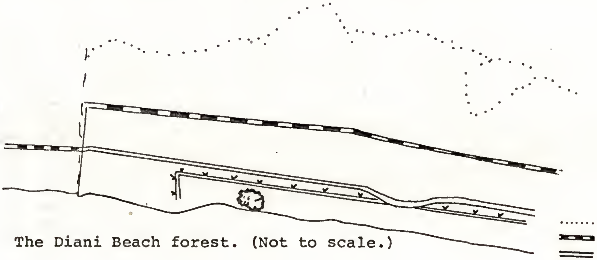


Fig. 4 The Diani Beach forest. (Not to scale.)

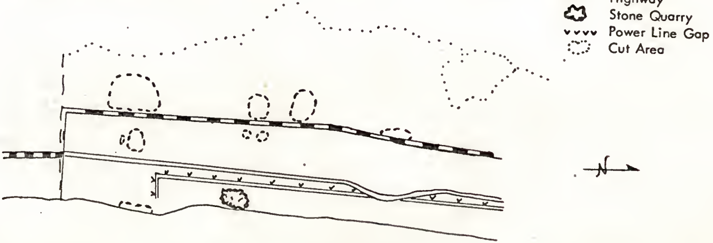


Fig. 5 The Diani Beach forest at the end of the project. (Not to scale.)

project: *Colobus angolensis palliatus* (colobus), *Cercopithecus mitis kibonotensis* (sykes), *Cercopithecus aethiops pygrathus* (vervet), and *Papio cynocephalus cynocephalus* (baboon). The taxonomic designation used here for the colobus follows Rahm ('70).

The ranges of these primate species (fig. 6), especially the vervets and the colobus, are apparently limited by their ecological requirements. The vervets were never actually found in the forest type IV proper, except in the small remnant between the Jadini Hotel and Bonham's, hereafter designated as Bonham's Forest. Throughout their distribution in this area, they tended to stay along the coastal margin, close to human habitation and the secondary floral association. The colobus, however, were limited by the presence of the primary association and were not found outside its boundary. North of the Jadini, the forest graded into secondary growth; at the southern edge, the boundary was abrupt and marked by a dirt road and extensive lantana thicket. The distribution of the colobus, however, did continue further south where there were patches of primary forest. The baboons moved in and out of the forest and area in general and were not frequently seen, especially at the inception of the project; this might have been due to the disruption of their normal routine by the construction of the highway. The sykes could be found in both the primary and secondary growth and probably had as large a range or distribution in the area as the baboons.

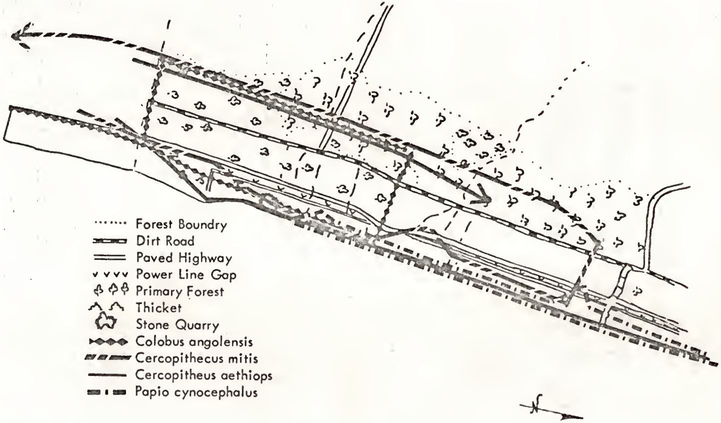


Fig. 6 Ranges of the four cercopithecoid species in the Diani Forest, November, 1972 - March, 1973. (Not to scale.)

The study site was found to be intensely utilized by one troop of seven colobus (T7 troop) to which an infant was born in November. There were at least two additional troops that could be seen at various times: a troop of three was occasionally seen in the northwest corner of the forest, just east of the power line; and a troop of about ten individuals usually was using the area around Mrs. Coverdale's property, but occasionally was known to move into Bonham's Forest which was included in the study site. Because of the nature of the project, it was not possible to identify individual colobus monkeys, but T7 troop was the only one to have a white infant present, and this was used as the distinguishing criterion.

One troop of *Cercopithecus mitis*, or sykes monkeys, was known to utilize the study site. Their range was considerably larger than that of the colobus. The *C. mitis* troop was the most difficult to habituate; it was only toward the end of the project that they could be approached and followed for prolonged periods. They were more habituated in some areas than others, and it often became necessary to predetermine their destination as they began to leave a site so that it could be reached prior to their arrival; if most of the troop arrived before the investigator, they usually dispersed quickly, often disappearing for long periods of time. The troop was estimated to have 18 to 22 members, but usually smaller groups of five or six were encountered or were visible. This pattern seems to be characteristic of the species, specifically, and of forest dwelling primates, in general, which are often screened from view by the foliage (Aldrich-Blake, '70). Only one sykes, an old female, was identifiable throughout the project.

The study area also included one troop (B's troop) of 14 vervet monkeys to which three infants were born between February and March. Several troop members were identifiable; a small juvenile, named "Scarbaby" because of a large scar widthwise across his back, was consistently used to identify the troop since the scar did not begin to fade until March.

A second vervet troop, the Two Fishes troop (2F troop), was studied. Their range overlapped that of B's troop in the northern portion of B's range. They were quickly habituated to the investigator, but were studied less than B's troop. Information obtained from the Two Fishes troop was used for supplementary and comparative purposes.

One baboon troop of about 13 members was using the area sporadically; it is possible that they were a splinter group from a larger troop of some 50 members who were frequently seen on the 4° 20' S road, in the lantana thicket, and on the most southern portion of the highway.

CHAPTER III

METHODS AND PROCEDURES

It was initially felt that the objective of the project, which was to investigate the differential utilization of the Diani Forest by the four cercopithecoid species, necessitated finding an area in which the ranges of all four species overlapped. An initial period of survey was conducted in the forest proper during which the general ranges of the species were determined by walking through the forest along the roads and transects and noting the place and time any monkeys were seen. Ultimately, a rough estimate of their ranges was determined (fig. 6)(§ 2) and only one well-defined place of overlap was observed. A decision was made to conduct the project at this location because the situation allowed a more complete understanding of the overlap, differentiation, and interaction of all four species simultaneously.

Spatial Utilization

Each troop was contacted and followed intensively and continuously for five to seven days each month depending on the degree of habituation they demonstrated. However, observations were made on them at times outside the period specifically designated for them due to the great degree of range overlap that occurred in this area as indicated in figure 7. Field observations were recorded on a tape recorder and rough field transcriptions made.

The particular place and time that a troop was first seen in the morning were noted and then their course followed each day; their movements and end points of movement were also noted. When a troop remained in one place for a prolonged period of time, periodic time checks were made indicating the behavior occurring at that time. The results of these data were plotted on an enlarged drawing of an area map which had been obtained at the government map office in Kenya. Since movements were usually nonrandom and centered around particular areas, key locations such as tamarind trees, gardens, or topographic features were marked on the map.

There are a number of methods for estimating the ranges of animals; the method used here is that proposed by Odum and Kuenzler ('55). Each noted location check was plotted on the map and these were then connected forming a polygon representing the month's range. The extreme outermost points were connected by straight lines so as to include all other points; this resulted in a larger area than would be given if all the points were connected individually, but it resulted in only one possible polygon giving a measure of the maximum range. Within the maximum range, areas were utilized differentially depending on the

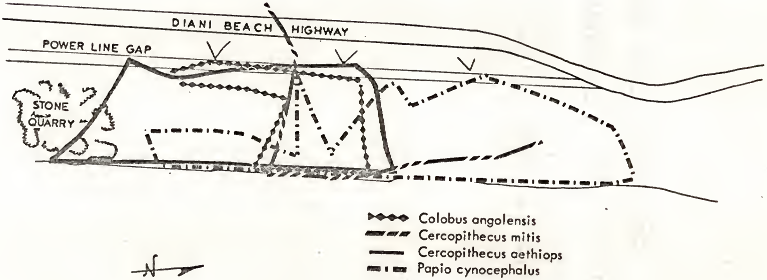


Fig. 7 Ranges of the four cercopithecoid troops at the study site. (Not to scale.)

distribution of relevant habitat features. These areas were determined by noting the number of times specific important behaviors, e.g., feeding, resting, playing, and sleeping, occurred. The total maximum range for each species during the study period was obtained by superimposing the monthly maximum ranges and, once again, connecting the outermost points.

It was most difficult to determine the vertical spatial utilization of the area by each species since the degree to which they were habituated to the investigator greatly affected this and often tended to skew their behavior toward a more arboreal distribution. Habituation of some of the troops, notably the sykes, was difficult because it was necessary to follow them as much as possible rather than remaining in on~~c~~e place and becoming a permanent "fixture" in the environment. The forest floor was covered with twigs and leaves in the dry season; thorns, nettles, and other spiney accoutrements were prominent features of the vegetation often making progression on the ground difficult and noisy for humans. Consequently, the vertical distribution remained unquantifiable throughout the project and was usually noted in broad qualitative terms.

Diet

Information concerning the diet of the monkeys was gathered in two ways; first, by the direct observation method and, secondly, by fecal analysis.

Direct observation. During the course of observed feeding behavior, all plants noted as being eaten were collected and preserved. The leaves, flowers if present, and, if possible, the fruits were dried in a plant press. Samples of the fruits were also preserved in a formol-acetic-alcohol solution (De Wolf, '68). These samples were used as a reference collection for analysis of the fecal material. Data concerning the species observed eating the plant, the part of the plant being eaten, the number of individuals eating it, the type of feeding behavior, i.e., casual or intensive, and the location, date, and time of observation were recorded and accompanied each specimen. The dried specimens were identified by Mr. Simon Mathenge of the University of Nairobi, Botany Department, and the East African Herbarium. One plant collection was deposited at the botany department of the University of Nairobi and another with the Florida State Museum in Gainesville, Florida.

Fecal analysis. It was anticipated that continuous monitoring of all animals would be impossible since feeding often occurred out of view of the observer in dense foliage. To ameliorate this difficulty, current methods of research on mammalian food habits are often based on analysis of stomach contents or fecal samples. While gastrointestinal investigations can be found in the primate literature (Fooden, '64; Jones, '70), they are limited by random availability of material and were considered inappropriate to a behavior study. Thus, collecting and analyzing fecal samples is the more reasonable method for primate studies and was used in this project.

Fecal samples were collected as soon as they could be obtained after the animal had defecated, thus only fresh or relatively fresh samples were collected. It was important to obtain a sample as quickly as possible to prevent excessive removal of fecal material by dung beetles, although sometimes up to half an hour elapsed before a sample could be reached without disturbing the animals excessively. In such cases, the sample was collected only if it was considered to be fairly intact.

A sample was never taken unless the species responsible was identified; this was especially important if two or more species were present in the area concurrently. Although some species specificity was noticed, it had the potential of being unreliable when diets converged. Each sample was placed in a plastic bag with a small amount of 10% formalin solution and assigned a number. Data concerning the species, time, location, date, and, if possible, the age and sex of the individual were recorded. In total, 164 samples were collected over the six-month period: 63 vervet, 35 sykes, 45 colobus, and 21 baboon samples.

The fecal samples were analyzed at the Florida State Museum laboratory where they were dried in a heated vacuum desiccator at 80° to 100° C for four to 12 hours, depending on the size and species of the sample. Once the sample was dried, a total sample weight was obtained using a metler balance. The sample was then macerated and macrosorted. A lamp, with a magnifying glass, and a microscope were used for further identification. Identifiable or recognizable material was sorted, weighed, and stored in vials. The determination of recognizable material relied most heavily on the reference collection, but some items, e.g., certain grasses, cultigens, and figs, were identified by Mr. David Hall of the University of Florida Herbarium. The data obtained from this analysis were used to qualitatively supplement the observed diet and are discussed individually as the material for each species is presented, as well as in the summary and conclusion chapters. The individual fecal smaples and their contents are listed in the appendix. The weight measurements were also used in a statistical analysis of the proportion of insect material eaten by the different species which is discussed in the appendix.

CHAPTER IV

THE COLOBUS

Relatively little is known of the ecology and social behavior of the African *Colobinae*, specifically the *Colobus angolensis* species. Morphologically the *Colobinae* are characterized by a large, sacculated stomach and long intestines, elongated hands and vestigial thumbs, and an enlarged larynx with laryngeal saccules and subhyoid sac opening into the larynx (Marler, '72). The enlarged sacculated stomach and elongated intestines have been related to a diet comprised of a high percentage of leaves. Bauchop and Martucci ('68) found that stomach contents of langurs (Asian *Colobinae*) contained fermentation end products, similar to those found in ruminants, and a high number of cellulose-digesting bacteria. The structure of the hand is thought to be correlated with locomotion, which in the colobus is characterized as arboreal quadrupedalism coupled with "flying leaps" from one tree to another. These leaps are executed with the elbows out, and individuals usually land feet first with their feet and hands close together (Kingdon, '71). Their clumsy appearance on the ground is probably due to the transference of these leaping motor patterns to the terrestrial medium.

The adaptation of the larynx is often seen to be correlated with specializations for sound production, especially the "roaring display." The colobus are generally characterized as being lethargic, unaggressive, and relatively silent animals who spend most of their time eating and resting. Their unique black and white coloration is most impressive, particularly in the *guereza* species.

The density of the colobus population in the Diani Forest appeared to be relatively high. Within the study site, at least three different troops could be distinguished; the area may also have been used to a much smaller degree by a fourth troop which was occasionally seen west of the power line gap at Bonham's. One troop, T7, was selected for study in this area. It appeared to use the forest most consistently; the area designated as Bonham's Forest was considered to comprise the core area of its home range. A second troop, T10, from Coverdale's, could also be found in Bonham's Forest and, sometimes, in close proximity to T7. Occasionally, the two troops appeared to join for short periods during the day.

T7 troop was comprised of two adult males, three adult females, and two juveniles. One white infant was born sometime in late October or early November, and a second was seen in February. For the most part, their behavior conformed with the behavior reported for other black and white colobus in the literature (Ullrich, '61; Schenkel and Schenkel-Hulliger, '69; Marler, '68, '72; Leskes and Acheson, '71; Groves, '73), although there were some differences. Most noticable among these differences was the apparent lack or infrequency of the roaring display (Walek, '72), and the level of social interaction seemed to be low. Relatively little grooming, play, or other social contact was seen.

The maximum home range for the T7 troop, for the period of November, 1972, through March, 1973, is illustrated in figure 8. This area encompassed a sector (Bonham's Forest) of type IV forest which was an area of natural forest with conspicuous coral outcropping, partially cleared for human habitation. A small section of forest, approximately 15 m wide, separated Bonham's property from Coverdale's property. The back part of this area contained primary forest association up to the boundary of the power line gap. This portion had been cleared in 1969 and, subsequently, became overgrown with *Lantana camara*, one of the predominant secondary growth species. Whenever the colobus were seen to leave the core area (fig. 9), they preferred to use the areas with primary association; however, they occasionally could be seen crossing the yard, which they always did via the trees which had been left there. As can be seen in figure 10, the size of the monthly maximum home range remained relatively small and

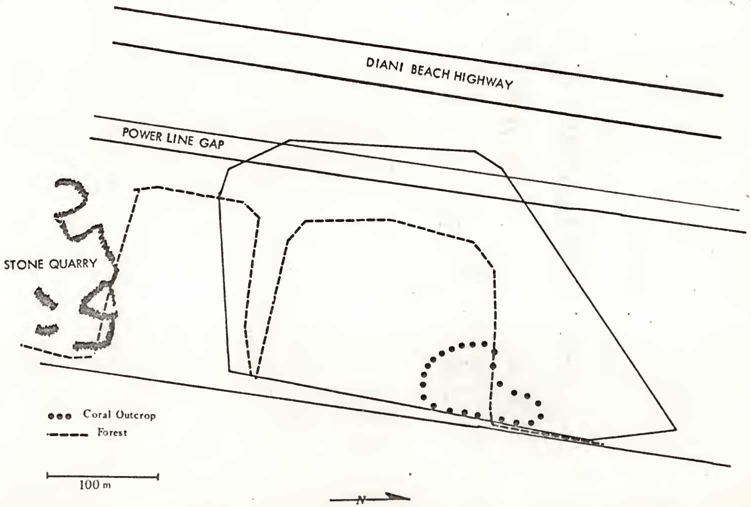


Fig. 8 Maximum home range of *Colobus angolensis* in this study site, T7 troop.

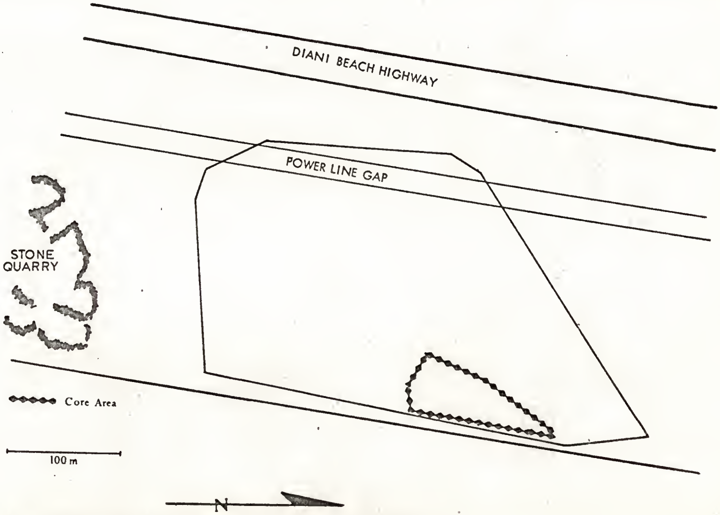
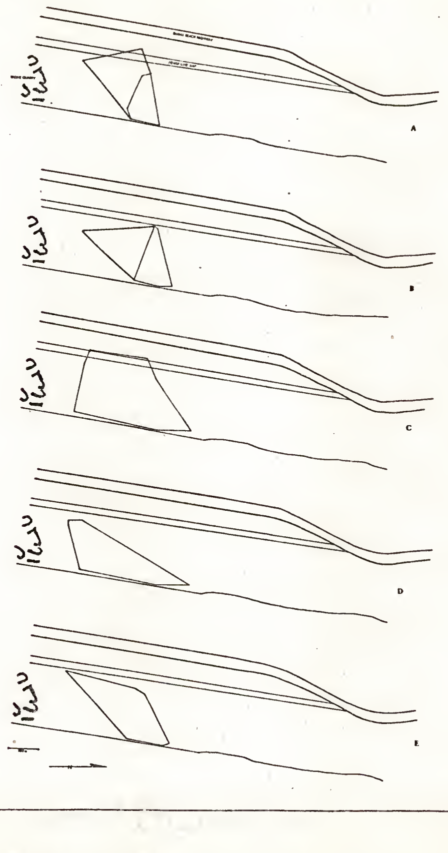


Fig. 9 Core area of *Colobus angolensis*, T7 troop.

Fig. 10 Monthly maximum ranges of *Colobus angolensis*, T7 troop. A-November, B-December, C-January, D-February, E-March; dotted lines indicate possible extension of the range based on occasional sightings of the colobus.


POWER LINE GAP
A
B
C
D
E
N

stable throughout the investigation and varied mainly in relation to areas outside the core area that contained food resources which were in season at that time.

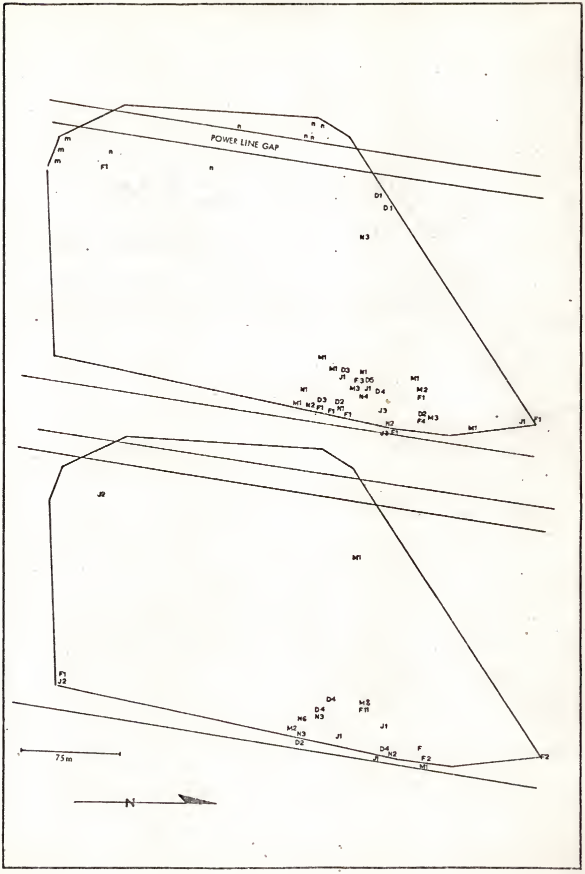
The colobus appeared to prefer the upper canopy, especially for traveling, although they were seen traveling in the lower canopy and on the ground. Occasionally, as the investigator sat quietly in the forest observing one of the other species, the colobus were seen running around on the ground. Most flight behavior was by means of the lower section of the upper canopy, but occasionally the troop ran to the ground.

Resting always occurred in the trees; particularly in the primary ramages (the thick branches leading off the trunk) and secondary ramages (close to the center of the trees). Resting sites (fig. 11) did not appear to be selected randomly; these were either areas consistently used for resting or trees in close proximity to a localized food source. The characteristic rest posture was either lying horizontally, with appendages dangling, or sitting hunched over, with legs drawn toward the body. They also rested in crotches between large limbs, leaning against the main part of the tree.

The sites of sleeping trees were not fully determined; most often, when the observation period ended, the troop was still in a feeding area, but feeding had ceased. However, they were not consistently in that spot the next

Fig. 11 Distribution of resting sites commonly used by *Colobus angolensis*, T7 troop. Months are indicated as: N-November, n-possible November, D-December, J-January, F-February, M-March, m-possible March. Numerals indicate the number of times a site was used.

Fig. 12 Distribution of feeding sites of *Colobus angolensis*, T7 troop. Months are indicated as: N-November, D-December, J-January, F-February, M-March.


POWER LINE GAP
n
n n
n n
m
m
m
n
F1
n
D1
D1
N3
M1
M1 D3
J1
N1
F 3 D5
M1
N1
M3 J1
N4
D4
M2
F1
M1 N2
D3
F1
D2
F1
N1
F1
J3
D2
F4 M3
N2
J3 F1
M1
J1
F1
J2
M1
F1
J2
D4
M8
F11
D4
N3
N6
M2
N3
D2
J1
J1
D4
N2
F
F2
J1
M1
F2
75m
N

day, although they often arrived shortly after the day's search for them began. Attempts to follow them after they left an evening feeding site usually resulted in flight behavior and their subsequent disappearance from the area.

Feeding occurred at all levels in the trees, in low bushes, and, infrequently, close to or on the ground. The distribution of feeding sites (fig. 12) remained concentrated in the coral outcrop area and primary forest (core area) throughout the six-month period; consequently, the troop did not move into other sections of the study site. This high ceiling of resource availability is characteristic of animals who rely heavily on foliage for food.

Two types of feeding behavior were observed: intensive and casual. Intensive feeding was characterized by three or more troop members eating the same items, at about the same time, over a prolonged period. Intensive feeding occurred in the early morning, roughly from 0600 h. to 0900 h., and in the afternoon, approximately 1400 h. to 1700 h. Casual feeding, on the other hand, was of short duration and appeared more haphazardly, taking on the form of an individual reaching out and eating some nearby item or moving to some food source in close proximity to a resting place. As indicated in table 4, the periodicity of feeding behavior remained stable during the two seasons (wet and dry) encompassed by the project.

TABLE 4

The feeding activity of the
Colobus angolensis, T7 troop

Time (h.)	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
0500						
0530						
0600						
0630			icc		ii	ic
0700			icc		iiic	i
0730			iicc		iiii	i
0800			i	i	i	i
0830				i	i	
0900					i	i
0930		i			i	i
1000		cc				i
1030		iccc	c	c		i
1100		c	icc			
1130				i	cc	
1200		c		i	c	c
1230				c		
1300					ic	
1330		i			ii	c
1400					i	
1430		cc	ic	c	iiiic	ic
1500			ii	icc	ii	i
1530		ic	iiiccc		iii	i
1600		iicc	iii		i	i
1630		ii	iiccc		ii	
1700		i			ii	
1730					i	
1800						

i represents intense feeding, i.e., three or more indiviuals.
c represents casual feeding, i.e., one or two individuals.

The diet of the colobus was characterized by lack of variety. A total of 31 items were collected after the colobus were observed eating them: 18 were identified to species; four were identified only as being in the genus *Ficus*; three were identified only to family; and, the remaining six are unidentified to date. These items are listed in table 5; the month in which they were observed eaten and the part eaten are also indicated. Certain items can be seen as the most important constituents of their diet. *Tamarindus indica* was utilized from November through March, but it was less important when the pods were being eaten than when the buds and leaves were consumed. *Drypetes gerrardii*, *Ficus sp.*, *Haplocoeum inoploeum*, and *Rhamnaceae* are the next important items. Table 6 shows the type of feeding behavior associated with each food item. The lack of variety is especially apparent on a daily basis; as can be seen in table 7, at most, five different items were seen eaten in one day, but usually there was less variation. The colobus were seldom seen drinking water; however, on one occasion, they were seen to lick leaves after a rainstorm.

As was expected, leaves comprised the bulk of the diet; however, fruit, leaves, buds, and flowers were also observed being eaten. Although the bulk of each fecal sample consisted of unrecognizable fragments of plant material,

TABLE 5

Plants observed being eaten by
Colobus angolensis, T7 troop

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Adansonia digitata	leaf				+°		
	bud				+	+	+
	flower					+	+
Afzelia quanzensis	leaf					+	+
Begonia meyeri-johni	fruit	+					
Capparis tomentosa	leaf						+
Combretum schumannii	leaf or seedcase		+				
**Cynanchum sp.*	leaf		+	+			
**Cyphostemma adenocaule*	leaf		+	+			
Drypetes gerrardii	leaf		+	+	+	+	
Ficus sansibarica	leaf		+	+			
Ficus sp. (poss. four different species)	leaf			+	+	+	+
Haplocoeum inoploeum	leaf	+	+	+	+		
**Hoslundia opposita*	leaf			+			
Lepisanthes senegalensis	fruit					+	+
Meliaceae	leaf		+				
Monanthotaxis fornicata	leaf					+	
**Premna hildebrandtii*	leaf		+				
Rhamnaceae	leaf		+	+	+		
Rutaceae	leaf	+	+				
Sideroxylon inerme	fruit/seed				+		+
Stadmannia sideroxylon	seed				+	+	
Tamarindus indica	pod/fruit		+	+	+		
	leaf					+	+
	bud					+	+
Tarenna nigrescens	leaf					+°	
Trichilia roka	leaf						+

+ represents month in which eaten.
* represents secondary association.
° represents possibility of being eaten.

TABLE 6

Type of feeding behavior associated with food items

Plant eaten	Type of feeding					
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Adansonia digitata					ccc	c
Afzelia quanzensis					i	i
Begonia meyeri-johni	i					
Capparis tomentosa						c
Combretum schumannii						c
Cynanchum sp.		c	c			
Cyphostemma adenocaule		c	c			
Drypetes gerrardii		iic	cc	c	ii	
Ficus sansibarica/leaf		ii/c	i			
Ficus sp.			ccc	i	cc	c
Haplocoeum inoploeum	ii	iiii icc	iicc	i		
Hoslundia opposita			c			
Lepisanthes senegalensis					i	i
Meliaceae		c				
Monanthotaxis fornicata					i	
Premna hildebrandtii		c				
Rhamnaceae		ic	iiicc	icc	c	
Rutaceae	c					
Sideroxylon inerme				c		i
Tamarindus indica-pod/bus/leaf		cc	iiii iccc	c	/iiii iiiii /c	/iii/ cc
Tarenna nigrescens					i	
Trichilia roka						c

i represents intense feeding, i.e., three or more individuals.
c represents casual feeding, i.e., one or two individuals.

TABLE 7

Daily variety in diet of *Colobus angolensis*

Month	Total # of days observed	Number of items eaten per day during intense observation period					
		1	2	3	4	5	6
October	3	3					
November	5	2			3		
December	5		3		1	1	
January	4	2		2			
February	5	2		2	1		
March	7	2	2	2	1		
	29						

often ground to a fine powder, the analysis on the macro-level proved invaluable in that it brought out the use of three items that were not observed being eaten and considerably changed the frequency and period of usage of another. As seen in table 8, the fruit of three species of figs were eaten, two in March and one in December. It is felt that these were not observed being eaten since the feeding most likely occurred in the thick foliage out of the observer's view. The seeds of *Sideroxylon inerme* are about the size of a pea and have a hard outer shell and pea-like inner part. They were only observed being eaten in January and March. The fecal analysis, however, showed that they were of considerable importance throughout the study period. There are apparently

TABLE 8

Identifiable plant and insect material in *Colobus angolensis*, T7 troop, fecal samples$^{\infty}$

Identifiable material in fecal samples	Part	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Plant:							
Ficus exasperata	seed			$+^{1}$			
Ficus populifolia	seed						$+^{2}$
Ficus sycomorus	seed						+
Sideroxylon inerme	seed/shell		$+^{1}$	$+^{4}$	$+^{7}$	$+^{6}$	$+^{7}$
Tamarindus indica	pod			$+^{1}$			
	bud					$+^{11}$	$+^{9}$
Insect:							
Hymenoptera Formicidae	gaster			$+^{1}$			
	head					$+^{3}$	
unidentifiable	frag.		$+^{1}$				$+^{2}$

+ represents month in which eaten.

$^{1-11}$ represents number of fecal samples.

∞ A piece of tympanic ring of small mammal found in sample #23, November 26, 1972.

two reasons for the discrepancy: first, the seeds grow off of small branches and are usually in the dense foliage, so that an individual could feed out of view of the observer; and, secondly, the colobus' lack of a thumb renders them incapable of plucking small round objects, thus necessitating the breaking of branches in order to bite off the berries. The high rate of appearance in the fecal material was probably due to morphological restraints on feeding behavior; the berries were apparently cracked in the mouth, the seed kernel chewed, and both seed and shell swallowed. This is in contrast to the sykes monkeys, who have well-developed thumbs and were seen eating these seeds by picking them off with their hands; almost no shell fragments were found in their fecal samples. Five fecal samples contained insect material that apparently had been eaten and digested (table 8). Insects were most likely ingested accidently when on leaves and chewed thoroughly; consequently, the actual amount of insect material consumed remains unknown.

CHAPTER V

THE SYKES

Cercopithecus mitis, the sykes or blue monkey, is widely distributed throughout Africa. The species tends to be most closely associated with a forest habitat, typically the evergreen forest. They are, also, found in montane and bamboo forests, savanna woodlands, and coastal mangrove swamps (Napier and Napier, '67; Gartlan and Brian, '68; Kingdon, '71). The distribution is generally discontinuous, which has resulted in numerous races displaying great variation in coloration, size, whisker length, and fur length. Local ecological conditions have apparently affected behavior to some degree, resulting in variations in diet, foraging behavior, and arborality. However, vocalizations, anatomy (which is evidently adapted to a uniform habitat), and "general disposition" are notably similar throughout the range (Gartlan and Brian, '68; Kingdon, '71).

The subspecies *C. mitis kibonotensis* was present at the Diani Beach forest. They had a mediumly thick blue-gray coat, black limbs, and black tail, and the amount of red coloration on the back varied considerably from one individual to another. They lacked a full white collar, but had a pale abdomen and neck with white tufts on cheeks and sometimes around the mouth. The population density appeared to be quite high throughout the area, and, as mentioned previously, they could be found in the forest, the secondary association, and along the coastal strip.

One troop, C's troop, was found to utilize the study area. What appeared to be another troop was sometimes seen at the northern edge of Bonham's Forest, but there was no apparent overlap; no intertroop interaction or association was seen between the two. The structure of C's troop conformed to that reported in the literature for blue monkeys by Aldrich-Blake ('70). During the months of November and December, it was common to see large numbers of sykes at one time; counts for C's troop varied between 18 to 22 members. After December, it was more common to see smaller groups, usually of five or six individuals. The fluctuations in group size apparently were a result of an adaptation toward flexibility in dispersion patterns correlated with feeding conditions. The actual composition of the troop was never completely determined, and only one individual, an old female, was recognizable. Solitary individuals, probably adult males, and one-male groups were seen. One infant was present in November and two more were born in March.

The maximum home range for the C's troop, for the period November, 1972, through March, 1973, is illustrated in figure 13. Considerable overlap occurred between the ranges of the sykes and colobus in the study site, especially in the core area of the colobus. The sykes range, however, continued southward for about 300 m, thus encompassing another section of primary forest. The maximum monthly range (fig. 14) showed a marked change in January, when utilization of the southerly extension increased considerably. During January, February, and March, however, the troop continued to use the entire range, often feeding in the southerly portion and resting in the areas used more intensively in November and December. The home range for the sykes contained two major core areas (fig. 15). The area designated "1" was utilized mainly in November and December. Core area "2" has been subdivided since concentrations of feeding sites were seen; area "2A" was mainly used in January, all of core area "2" in February, and "2B" in March. It is possible that the use of the term "foci of activity," which is often applied when there are several such small, scattered areas within a home range, would be more appropriate for *C. mitis* here (Bates, '70).

The genus *Cercopithecus* is considered to be mainly arboreal, and the sykes are most frequently reported as such. At Diani, the actual degree of arborality was never

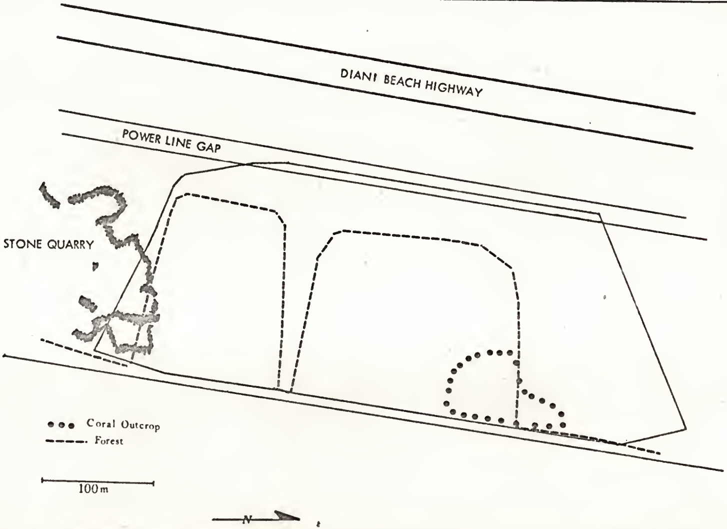
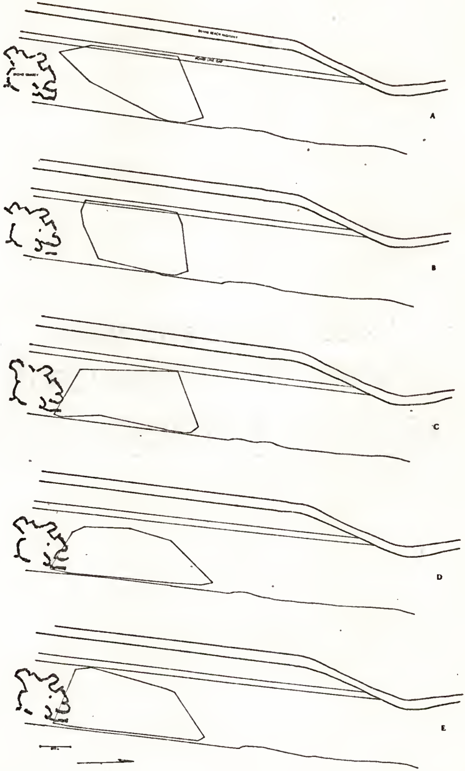


Fig. 13 Maximum home range of *Cercopithecus mitis*, C's troop, in the study site.

Fig. 14 Monthly maximum home ranges for *Cercopithecus mitis*. C's troop. A-November, B-December, C-January, D-February, E-March.


A
B
C
D
E

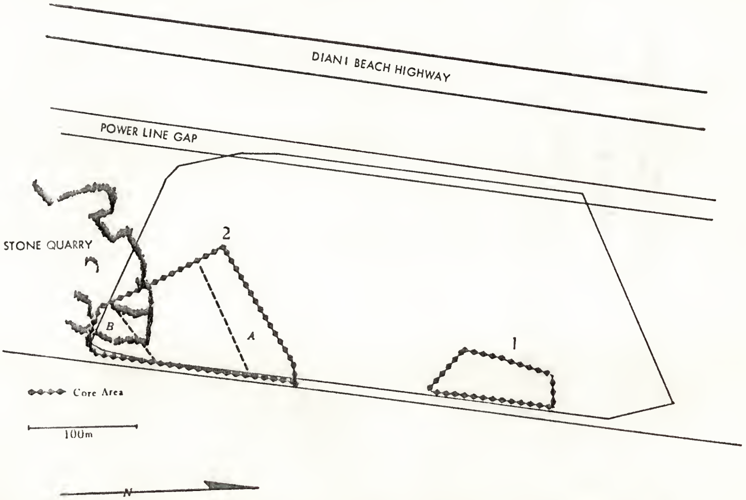


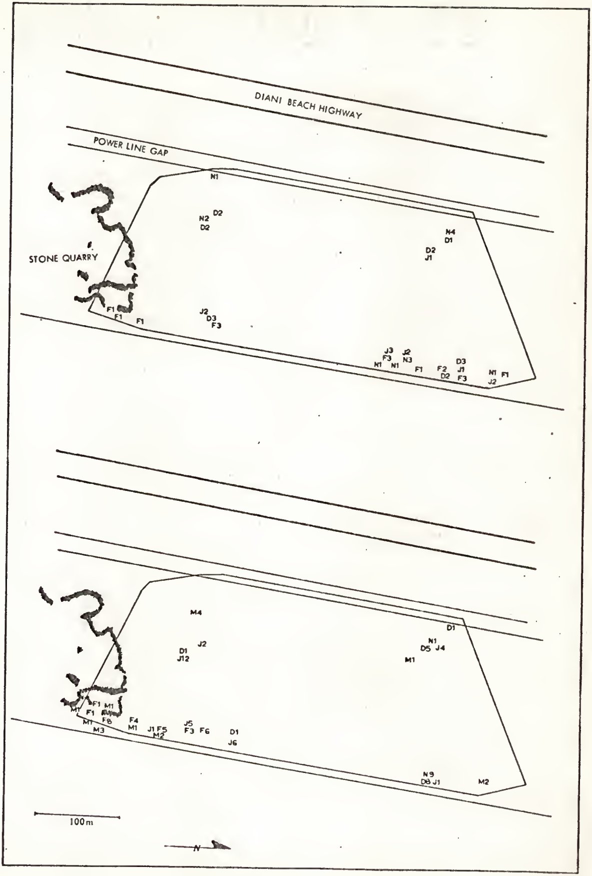
Fig. 15 Core areas of *Cercopithecus mitis*, C's troop, at the study site.

satisfactorily determined. The sykes were the most difficult to habituate, and the investigator's presence initially was the focus of considerable threat behavior and subsequent flight. Gradually, however, they adjusted to the investigator; first, as a fixed object and, eventually, as a moving one. Flight was always arboreal and usually in the lower upper story along thick branches. During normal progression, the troop did not move as a compact, integrated unit. Travel occurred in the trees and on the ground, both in the forest and in cleared areas; however, usually only the adults and, most frequently, the adult males traveled on the ground. It was believed that within the forest, terrestrial behavior was more frequent than observed. On numerous occasions, when the observer was quietly sitting stationary waiting for their arrival, a number of individuals entered the area via the ground. Feeding occurred on the ground and in trees, but was more frequent in the trees.

Resting sites (fig. 16) appeared to be relatively consistent, although this period was one of the most difficult in which to locate them. They could be seen resting for prolonged periods during the day, usually late morning to midafternoon. Resting occurred both in the trees and on or close to the ground on logs or coral boulders. Arboreal resting was usually in the primary and secondary ramages. The characteristic rest posture was

Fig. 16 Distribution of resting sites commonly used by *Cercopithecus mitis*, C's troop. Months are indicated as: N-November, D-December, J-January, F-February, M-March. Numerals indicate the number of times a site was used.

Fig. 17 Distribution of feeding sites commonly used by *Cercopithecus mitis*, C's troop. Months are indicated as: N-November, D-December, J-January, F-February, M-March. Numerals indicate the number of times a site was used.


DIANI BEACH HIGHWAY
POWER LINE GAP
STONE QUARRY
N1
N2 D2
D2
N4 D1
D2 J1
F1
F1
F1
J2 D3 F3
J3 F3
J2 N3
N1
N1
F1
F2 D2
D3 J1 F3
N1 F1
J2
M4
J2
D1 J12
D1
N1
D5 J4
M1
F1 M1
M1
F1
M1
F8
M3
F4 M1
J1 F5 M2
J5 F3
F6
D1 J6
N9 D8 J1
M2
100m
N

sitting, usually with the legs dangling or flexed, but not drawn close to the body as in the colobus. The sites of sleeping trees were never determined. In the evening, the troop was most often seen crossing the power line gap in the western portion of Coverdale's yard.

The distribution of feeding sites (fig. 17) was not constant throughout the study period; this was correlated with reliance on food items that were seasonal in nature. The presence and availability of food resources had a wide ranging effect on *Cercopithecus mitis*' range size, area utilization, and behavior. The most wide ranging effect was seen in the pattern of differential dispersion of troop members. Under typical feeding conditions, the troop was scattered, and small groups often foraged independently of one another. When the food supply was concentrated and localized, however, the entire troop fed together.

Feeding usually occurred in intensive bouts during the day. The data in table 9 indicate that a possible shift in feeding periodicity occurred concurrent with the shift in the feeding pattern mentioned; however, data from November and December were not obtained as frequently due to the limited habituation of the troop. During this period, the observer was usually situated in specific predetermined places in the study site rather than following them from one place to another. This period,

TABLE 9

The feeding activity of the *Cercopithecus mitis*, C's troop

Time (h.)	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
0500						
0530						
0600						i
0630			i	ii	i	i
0700		i	i	iis	iiss	i
0730		i	i	iiii	isss	
0800		i	sss	iiiis	iiis	i
0830		i		iss	is	i
0900			i	is	iii	i
0930			is		iis	
1000		i	ii		iii	
1030			iii		iii	
1100		i	iis		ii	
1130		ii	ii		i	ii
1200		iii	iiiss			ii
1230		iiii	iiiss			i
1300		i	s	i		i
1330		is	ss	iii	iiiii	i
1400			i	iiiiiis	iiiiis	i
1430			ii	iiiiiis	iiiiiis	
1500			iii	iiiii	iiiiis	ii
1530			ii	iii	iiiis	iiiis
1600		i	i	iiis	ii	iis
1630				iiis	i	i
1700				i	i	i
1730					i	i
1800						

i represents intense feeding; most of troop or visible group.
s represents small number of individuals visible.

the wet season, had a concentration of feeding behavior during 1030 h. to 1230 h.; feeding in the dry season occurred most intensively from 0630 h. to 0930 h. and, again, from 1330 h. to 1700 h.

The diet of the sykes was comprised mainly of fruits; seeds, flowers, leaves, and insects were also eaten. Thirty different plant items were observed being eaten by the sykes (tables 10 and 11). Among the items eaten by C's troop, seven were eaten during one month, six during two months, two for three months, one for four months, and only one, *Tamarindus indica*, for the entire study period. This pattern made the sykes appear to be "focal feeders," i.e., relying heavily on a few items for most of the time and supplementing this main diet with important, but seasonal, items. The most heavily relied on item was *Tamarindus indica*, which was eaten every month and consistently comprised the main protion of the day's diet. The fruit was most intensively eaten in November, December, and to a lesser degree in January. This was the period during which large numbered groups of sykes were seen feeding in a tamarind tree. At least three different tamarind trees were fed on for pods; the one most consistently eaten from was in the southeast portion of Bonham's Forest. During February and March, when the leaves and buds were eaten, different tamarind trees were utilized. Table 12 shows the number of different items

TABLE 10

Plants observed being eaten by
Cercopithecus mitis, C's troop

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Adansonia digitata	bud/case					+	+
**Begonia meyeri-johni*	fruit	+					
**Cissus rotundifolia*	leaf				+		
*Commiphora zanzibarica***	seed	+					
Dalbergia melanoxylon	seed	+		+			
*Ficus exasperata***	fruit		+				
Ficus populifolia	fruit						+
*Ficus sonderi***	fruit					+	
*Ficus sycomorus***	fruit		+				
**Hyphaene coriacea*	fruit						+
Lannea stuhlmannii	fruit				+		+
Lecaniodiscus fraxinifolius	seed		+		+		
*Lepisanthes senegalensis***	fruit						+
*Markhamia zanzibarica*** (poss. *hildibrandtii*)	bud	+	+	+			
**Pseuderanthemum hildebrandtii*	flower		+	+	+		
Sideroxylon inerme	seed/leaf			+	+	+	+
Suregada zanzibarensis	fruit					+	+
Tamarindus indica	fruit		+	+	+		
	bud/leaf					+	+
Ziziphus mucronata	fruit					+	+

+ represents month in which eaten.
* represents secondary association.
** represents eaten by different *C. mitis* troop.

TABLE 11

Cultigens and ornamental plants observed eaten by *Cercopithecus mitis*, C's troop

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Annona squamosa	fruit					+	
Annona reticulata	bud		+				
*Azadirachta indica***	fruit					+	
Caesalpinia pulcherima	seed				+		
Carica papaya	fruit			+			
Chrysophyllum cainito	fruit					+	+
Manilkara obovata	fruit			+	+		
Manilkara zapota	fruit					+	+
*Psidium guava***	fruit	+			+		

+ represents month in which eaten.
** represents eaten by different *C. mitis* troop.

TABLE 12

Daily variety in diet of *Cercopithecus mitis*

Month	Total # of days	Number of items eaten per day during intense observation period					
		1	2	3	4	5	6
October							
November	6	4	2				
December	7	2	4	1			
January	6			3	2	1	
February	6			2	2	2	
March	4		1	1		1	1

eaten per day each month during the intensive observation period. Once again, there was more variety in the diet during the time period when tamarind fruit was scarce or not in season; thus, when the troop was most dispersed. However, the data obtained in the first three months was to some degree affected by lack of habituation.

A seasonal comparison of the fecal samples was not possible, because samples were not obtained from the sykes during the first three months of the investigation. Most of the material recorded for the *C. mitis* samples (table 13), however, was material that was not observed being eaten; thus, the analysis was invaluable and greatly served to amplify the observed data. The analysis was, also,

TABLE 13

Identifiable plant material in
Cercopithecus mitis, Ç's troop, fecal samples

Identifiable plant material in fecal samples	Part	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Ficus exasperata	seed					$+^{1}$	$+^{3}$
Ficus populifolia	seed						$+^{2}$
Ficus sonderi	seed				$+^{1}$		
Ficus sycomorus	seed					$+^{1}$	
Ficus sp.	seed				$+^{1}$		$+^{2}$
Grewia goetzeana	seed			$+^{1}$	$+^{3}$		
Lantana camara	seed			$+^{1}$	$+^{1}$		
Lepisanthes senegalensis	seed						$+^{1}$
Manilkara sansibarensis	shell				$+^{2}$		
Sideroxylon inerme	seed shell			$+^{1}$	$+^{1}$	$+^{2}$	$+^{4}$
Stadmannia sideroxylon	seed					$+^{1}$	
Tamarindus indica	pod shell				$+^{1}$	$+^{1}$	
	seed residue				$+^{11}$	$+^{1}$	
	bud					$+^{7}$	$+^{10}$
Ziziphus mucronata	seed						$+^{7}$

+ represents month in which eaten.
$^{1-11}$ represents number of fecal samples.

TABLE 14

Identifiable insect material in
Cercopithecus mitis, C's troop, fecal samples

Identifiable insect material in fecal samples	Part	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Coleoptera Buprestidae	frag.				$+^{1}$		
Coleoptera Chrysomellidae	frag.					$+^{1}$	
Coleoptera Curculionidae	elytra				$+^{1}$		$+^{1}$
Hemiptera/Homoptera	nemelytra				$+^{1}$		
Hymenoptera Formicidae	legs/ gaster/ head/ wings			$+^{1}$	$+^{4}$	$+^{4}$	$+^{5}$
Hymenoptera Holyetidae	frag.					$+^{1}$	
Orthoptera Acrididae	frag.				$+^{2}$	$+^{1}$	$+^{1}$
Orthoptera Tettigonidae	frag.				$+^{1}$		
tick (Arachnida, Acarina)	frag.						$+^{1}$
unidentifiable fragments				$+^{1}$	$+^{4}$	$+^{5}$	$+^{8}$

+ represents the month in which eaten.
$^{1-8}$ represents the number of fecal samples.

important in that very little insect material was observed being eaten, but insect fragments, which were considered to be remains of digested insects, were present in a large number of the samples (table 14). Most of the insect remains that were identifiable were ant and grasshopper parts; however, considerable amounts were so fragmented that identification was not possible. The fecal samples for *C. mitis* often were quite similar in color and texture to those of the colobus; therefore, it is quite possible that leaves comprised a larger part of the diet than the study indicated. The application of a comparative microscopic analysis would be of great value in this situation.

CHAPTER VI

THE VERVETS

Cercopithecus aethiops, the vervet monkey, is one of the more widely distributed and abundant of the African cercopithecines. The geographic range of *C. aethiops* extends from the highlands of Ethiopia and semiarid regions of the Sudan to southern South Africa and from Senegal to Somali. Frequently found in the savanna habitat, they also occur in woodland, riverine gallery, lakeshore and thorn forests, temperate grasslands, and scrub areas. The forests do not appear to be inhabited homogeneously since the vervets tend to prefer the fringe areas (Tappen, '60; Gartlan and Brian, '68; Kingdon, '71).

The vervets appear to be equally adapted to terrestrial and arboreal habitats, and they spend a great deal of time on the ground. They are intermediate in anatomical adaptations to terrestrial habitat, falling between the arboreal cercopithecines and the terrestrial patas monkeys, to which they are closely related. The anatomical features of upper and lower arm length, ratio of foot to lower leg length, and lower leg to upper leg length seem to indicate that the terrestrial specializations are not similar to, or representative of, those of a primitive stock from which terrestrial forms developed from arboreal forms. Instead, vervet anatomy appears to be the result of adaptation to a nonuniform environment where there are considerable accessibility to and variability in vertical spatial utilization (Gartlan and Brian, '68).

The vervet is one of the smaller members of the genus *Cercopithecus*. The fur is a yellowish to olive color on the shoulders, back, and tail, while the outer lower surface of the limbs is black, as is the face. There is a ring of white fur around the face, and white ear tufts are frequently present. The male genitalia are brightly colored, usually turquoise in the adult, purple in the subadult and juvenile. Vocal and visual communication are well developed (Struhsaker, '67b), and troop structure is usually quite stable.

At Diani, the vervet population remained along the coastal strip. One exception to this was a number of vervets seen west of the Diani highway in the secondary scrub. The sighting occurred behind one of the hotel properties, and it is quite possible that they had moved into that area as a consequence of retribution from the hotel staff for their raiding of the facilities.

One troop (B's troop) of 13 or 14 vervets utilized the study site. This troop was composed of two adult males, four adult females, and seven subadults and juveniles. In March, three infants were present bringing the total to 17, but one infant disappeared just after the project ended. A second troop of vervets (2F troop) overlapped B's troop at the northern part of B's range. This troop was similar in composition, having three adult males, two or three adult females, and six or seven subadults and juveniles. One infant was born in late February. The 2F troop was studied during the project; often the time allotted to vervets was divided between the two troops. This was done mainly because of the investigator's inability to distinguish them during the first two months of the study; and, afterwards, because it was felt that comparisons between them might add further information on habitat partitioning, since the 2F troop was not in contact with baboons or colobus monkeys and did not have a stand of primary forest in their home range. The material on the diet of the 2F troop is listed separately.

The maximum home range for B's vervet troop for the period November, 1972, through March, 1973, is illustrated in figure 18. In the southern portion of the vervet range, there was considerable overlap with the colobus and sykes troops. The northern section was primarily cleared of climax forest and consisted mainly of a hotel complex and two private homes. Some trees had been left, and the secondary association had taken over wherever it had been

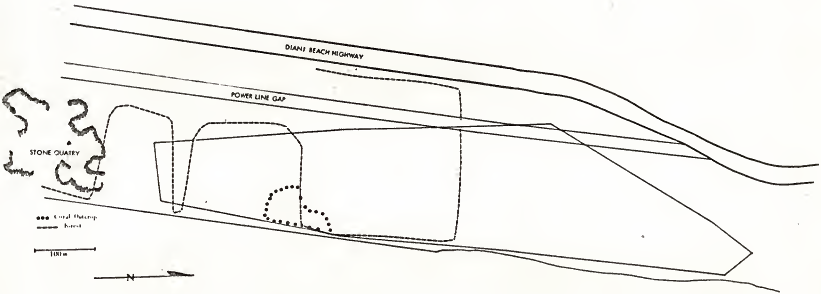
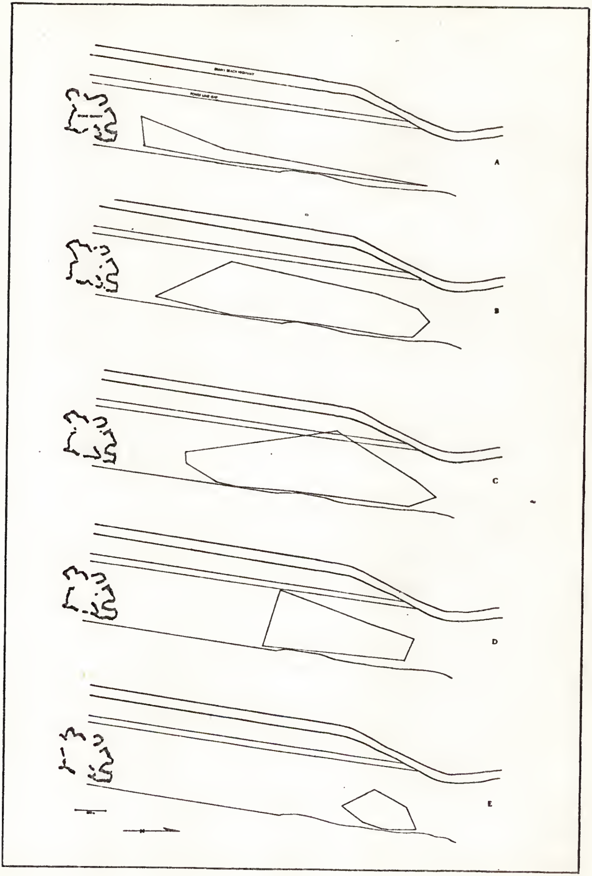


Fig. 18 Maximum home range for *Cercopithecus aethiops*, B's troop, in the study site.

permitted. Ornamental trees and shrubs and some cultivated plants, such as banana *(Musa sp.)*, papaya *(Carica papaya)*, custard apple *(Annona squamosa)*, guava *(Psidium guava)*, and tomato *(Lycopersicon esculentum)*, were planted in this area. The maximum monthly ranges (fig. 19) varied considerably over the six-month period. The major change occurred in January, at which time the troop ceased utilizing the southern portion of their range, thus no longer appearing in the major portion of the study site. They did, however, continue to use the northernmost portion of Bonham's Forest in February. The use of the northern section of the range appeared to be more consistent and stable and included trees that were most frequently used for sleeping. The southern portion, from Bonham's Forest on, contained several important seasonal dietary items. The situation was complicated by construction at the Jadini Hotel which lasted from October until the end of December. There is no doubt that this affected the troop's behavior considerably and possibly increased the amount of time that was usually spent in the southern part of their range.

The vervets were equally at home in the trees as on the ground. Movement through the home range occurred in both mediums; in areas where there were a lot of people, they seemed to prefer the trees. Human reaction to the vervets differed considerably. The tourists and private home owners tolerated and even enjoyed them, often feeding

Fig. 19 Monthly maximum home ranges for *Cercopithecus aethiops*, B's troop. Months are indicated as: A-November, B-December, C-January, D-February, E-March.

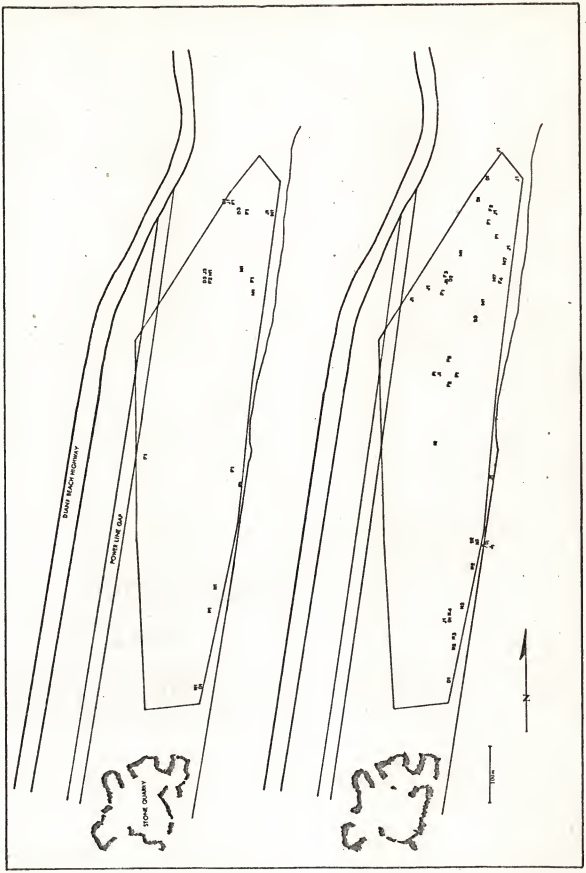

BEACH HIGHWAY
POWER LINE GAP
STONE QUARRY
A
B
C
D
E
N

the animals. Individuals who resided at the coast, or visited there, frequently appeared quite familiar with the troops, were aware of their behavior and movement patterns, and showed considerable concern over their fate in the area. On the other hand, the owners and managers of the hotels and, consequently, the staffs showed a general dislike for them. B's troop was particularly disliked; the managers had asked the game department to shoot the animals in 1970-71 and were talking of doing so again in 1973. Thus, in these areas, the vervets often traveled in the trees, but were not inhibited from moving and foraging on the ground. Play also occurred both on the ground and in the trees, and they usually utilized them consecutively, running on the ground, into the trees, and then jumping back onto the ground.

Resting sites appeared to be relatively stable throughout the study period, especially in the northern part of the range (fig. 20). Resting appeared to take on more of a consistent pattern in January; from this time on, the whole troop would recede into a thicketed scrub area and rest for a period of several hours, anywhere from 0900 h. to 1200 h. This behavior was seen to a lesser extent in November and December in the southerly part of the range; but more frequently, the troop was scattered and feeding more interspersed. This might have been due to the relative decrease in available food, since this

Fig. 20 Distribution of resting sites commonly used by *Cercopithecus aethiops*, B's troop. Months are indicated as: N-November, D-December, J-January, F-February, M-March. Numerals indicate the number of times a site was used.

Fig. 21 Distribution of feeding sites commonly used by *Cercopithecus aethiops*, C's troop. Months are indicated as: N-November, D-December, J-January, F-February, M-March. Numerals indicate the number of times a site was used.


DIANI BEACH HIGHWAY
POWER LINE GAP
STONE QUARRY
N
100m

period coincided with the hotel construction. Resting always occurred in the trees. Favorite resting sites appeared to be isolated clumps of small trees, six to 12 m high and rarely more than a meter in diameter. Vervets rested in sitting and reclining postures and favored the primary and secondary ramages close to the main tree trunk. One area, a small clump of such trees used for a midday resting place, was the most frequently chosen sleeping area (fig. 20).

Feeding sites (fig. 21) were widely distributed throughout the range, both within an observation period and throughout the period of the project. This had the effect of reducing their distinctiveness, particularly in October, November, and to some degree in December, when feeding appeared to be scattered and more individual. Consequently, feeding appeared to occur throughout the day. For January, February, and March, more distinct feeding periods were seen (tables 15 and 16), but the behavior pattern of fairly dispersed individuals feeding on a number of items was maintained; exceptions to this occurred when particular trees were in fruit. While this was somewhat reminiscent of the pattern seen in *C. mitis*, the overall distribution of individuals was different since there was less grouping tendency; this was probably related to the more scattered distribution of the resources.

TABLE 15

The feeding activity of the
Cercopithecus aethiops, B's troop

Time (h.)	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
0500						
0530						
0600			i			
0630					iii	ii
0700			i	i	i	i^{F}
0730			i		ii	iii
0800			^{F}	i		ii
0830			^{F}	i	i	
0900				ii	i	is
0930			ii	ii	is	
1000			i	ii		
1030		i	i^{F}	i	s	
1100		ii	s			
1130		ii	^{F}			iiis
1200		i	i	is	i	i
1230		i	i	i	i	i
1300		is	iii		i	s
1330		i			ii	i
1400		iii	i	i	ii	ii
1430		ii	i	i	i	i^{F}
1500			i	i	iii	ii
1530		i	i		ii^{F}	i
1600		i	ii	ii	ii	iii
1630		i	iii	i	ii	
1700		i				
1730		i				
1800						

i represents intense feeding; most of troop or visible group.
s represents small number of individuals visible.
F represents fed by humans or stolen from garbage.

TABLE 16

The feeding activity of the
Cercopithecus aethiops, 2F troop

Time (h.)	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
0500		i				
0530						
0600						
0630						
0700			i	i	i	
0730		i	i	i	ii	
0800		i	i		i	
0830				i		
0900		i				
0930			ii			
1000		i	i			
1030				i		
1100		i	ii	ii	i	
1130		ii		i	i	
1200		ii	i			
1230		i	i	i	i	
1300		i	i	i	i	
1330				i		
1400		i	i			
1430		ii	i	iii	i	
1500		i	ii			
1530		iii	ii	ii	ii	
1600		ii	ii			
1630			i	i	i	
1700		i	i	i	i	
1730		i	i	i	ii	
1800						

i represents intense feeding.

The diet of the vervets was characterized by considerable variety (table 17); it was common to see four or more items being eaten in a day. The number of different

TABLE 17

Daily variety in diet of *Cercopithecus aethiops*, B's troop

Month	Total # of days	Number of items eaten per day during intense observation period											
		1	2	3	4	5	6	7	8	9	10	11	12
October													
November	5	3			1				1				
December	4		1	1	1				1				
January	3								1			1	1
February	4						1	1				2	
March	4			1			1	1				1	

items eaten per day increased from January on, once again, reminiscent of the pattern seen in *C. mitis*; but the change appeared to be more subtle, and the average number per day consistently exceeded that of *C. mitis*. A total of 58 different plants were observed being eaten by B's troop (table 18): 27 of these plants were considered to be indigenous to the area; 13 of these were not components of the primary association, but more likely of the secondary association; and, the other 18 plants that were consumed

TABLE 18

Plants observed being eaten by
Cercopithecus aethiops, B's troop

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
*_Abutilon mauritianum_	flower/bud poss. seed		+	+	+		
*_Alysicarpus rugosius_	?					+	
*_Begonia meyeri-johni_	fruit				+		
Carpodiptera africana	seed		+				
Dalbergia melanoxylon	seed	+	+				
Ficus depauperata	fruit			+			
Ficus exasperata	fruit			+			
Ficus sonderi	fruit					+	
Ficus sycomorus	fruit			+	+	+	
*_Grewia goetzeana_					+		
*_Hoslundia opposita_	?	+					
*_Jasminum abyssinicum_	leaf				+		
*_Lablab purpureus ucinatus_	flower/ seed						+
*_Lablab sp._	flower/ seed			+	+		
Lannea stuhlmannii	seed/leaf/ stem				+		+
*_Lantana camara_	seed			+	+		
Lepisanthes senegalensis	fruit						+
*_Pandanus sp. (?kirkii)_	fruit						
*_Phyllanthus sp._	fruit					+	
*_Pseuderanthemum hildebrandtii_	flower				+		
*_Securinega virosa_	seed					+	
Sideroxylon inerme	seed		+				
Tamarindus indica	fruit		+				
Thunbergia holstii	?	+					
*_Vigna membrenaceace_	seed		+	+	+		

+ represents month in which eaten.

* represents secondary association.

were either ornamental trees or shrubs or cultigens (table 19). Fruits, seeds, buds, and flowers were eaten; only rarely were leaves and grass eaten. While foraging on the ground, shuffling of leaves, and manipulation of the forest litter or other debris was frequently seen, only four incidences of definite insect eating were recorded; three occurred on one day in February, and one in March. This relative paucity of observed insect consumption was surprising. The vervets were observed drinking water from faucets at the hotels and near private homes, but a natural water source was never found in their area.

The vervets of the 2F troop displayed a feeding activity pattern (table 16) similar to that of B's troop. Thirty-five different plants were observed being eaten (tables 20 and 21): 19 of these were indigenous to the area; seven of the indigenous plants were from secondary association; and, 16 were ornamental plants. The home range of the 2F troop did not contain a stand of type IV forest, but some trees had been left in the area; these were well dispersed and had probably been left for their value as shade trees. *Tamarindus indica, Ficus sp.,* and *Lecanodiscus fraxinifolius* seemed to be favored. These vervets had more access to tamarind trees, and there was little interspecific competition for them, except with a

TABLE 19

Cultigens and ornamental plants observed eaten by *Cercopithecus aethiops*, B's troop

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Ananas comosus^F	fruit		+	+	+	+	+
Annona squamosa (custard apple)	fruit		+	+	+		
Averrhoa carambola	fruit				+		
Azadirachta indica (neem)	fruit					+	+
Bougainvillea spectabilis	pulp of young stem		+		+	+	+
Caesalpinia pulcherrima	seed/pulp	+		+	+	+	
Carica papaya^F (papaya)	fruit			+	+	+	+
	leaf-rare						+
Chrysophyllum cainito (star apple)	fruit						+
Citrus limon^F (lemon)	fruit	+					
Citrus paradisia^F (grapefruit)	fruit				+	+	
Citrus sinensis^F (orange)	fruit					+	+
Cocos nucifera^F (coconut)	fruit				+	+	+
Daucus carota^F (carrot)	root					+	
Delonix regia	seed	+					
Lycopersicon esculentum (tomato)	fruit	+	+		+		
Mangifera indica^F (mango)	fruit		+				+
Manilkara obovata	fruit			+			
Manilkara zapota	fruit					+	+
Musa sp. (banana)	fruit					+	+
Psidium guava (guava)	fruit	+		+	+	+	
bread		+				+	+
posha					+	+	+

+ represents month in which eaten.
F represents fed to vervets by humans or taken from garbage.

TABLE 20

Plants observed eaten by *Cercopithecus aethiops*, 2F troop

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
**Abutilion mauritianium*	flower/bud				+	+	
**Begonia meyeri-johni*	fruit		+				
**Boehaarvea erecta*	root				+		
Cordia sp.	bud			+			
Drypetes natalensis	fruit			+			
Ficus depauperata	fruit					+	
Ficus exasperata	fruit	+	+	+			
Ficus sycomorus	fruit		+	+			
Ficus sp.	fruit				+		
**Grewia goetzeana*	fruit	+					
**Grewia plagiophylla*	fruit				+	+	
**Lablab*	seed/flower		+	+			
Lannea stuhlmanni	fruit				+		
**Lantana camara*	seed	+	+	+	+		
Lecanodiscus fraxinifolius	fruit		+				
Sideroxylon inerme	seed				+		
Tamarindus indica	fruit		+	+	+		
Terminalia capatta	fruit		+				
Ziziphus Mucronata	fruit					+	

+ represents month in which eaten.
* represents secondary association.

TABLE 21

Cultigens and ornamental plants observed eaten by *Cercopithecus aethiops*, 2F troop

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Anacardium occidentale	fruit		+		+		
Ananas comosus[F]	fruit		+			+	
Annona squamosa	fruit				+	+	
Bougainvillea spectabilis	pulp of young stems	+	+	+	+		
Caesalpinia pulcherrima	seeds	+	+	+	+		
Capsicum fructescens		+					
Carica papaya[F]	fruit		+		+	+	
Citrus limon[F]	fruit	+					
Citrus paradisia[F]	fruit			+		+	
Citrus sinensis[F]	fruit		+	+			
Cocos nucifera[F]	seed	+		+	+	+	
Cucumis sativus[F]	fruit		+				
Delonix regia	seeds				+		
Musa sp.[F]	fruit	+		+		+	
Pandanas kirkii	fruit	+		+	+		
Psidium guava	fruit				+		

+ represents month in which eaten.
F represents fed by humans or stolen from garbage.

few sykes that inhabited the area. Consequently, the 2F troop utilized tamarind more frequently and over a longer time period. The choice of ornamentals and cultigens varied from one house to another, and there was more variation between the two troops in this category. Furthermore, the Two Fishes Hotel staff, who were in the 2F troop range, did not harass the monkeys as much as the Jadini Hotel staff. Also, the constant stream of tourists at the hotel provided a large portion of the food for the vervets. They were fed more frequently and consistently than B's troop. Such items as bananas, citrus fruits, and coconuts were handed out in fairly large quantities in the early morning and at tea time (1600 h. to 1700 h.). It was not uncommon for hotel guests to be awakened by the vervets banging on the roof of the rooms as they ran across the roof top, and some vervets were bold enough to enter open rooms and steal fruit.

The analysis of the vervet fecal samples (table 22) did not greatly amplify the plant items observed eaten. Actually, the greatest value here was in extending the period over which some of the items were eaten; *Lantana camara, Sideroxylon inerme,* and *Ficus exasperata* are examples of this. Another way, and perhaps the most important, was the information obtained on the insect component of the diet as shown in table 23. Insect material was found in fecal samples from December through

TABLE 22

Identifiable plant material in
Cercopithecus aethiops, B's troop, fecal samples

Identifiable plant material in fecal samples	Part	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Azadirachta indica	seed						$+^{2}$
Begonia meyeri-johni	seed				$+^{2}$		
Drypetes natalensis	seed				$+^{1}$		
Ficus depauperata	seed			$+^{4}$	$+^{1}$	$+^{4}$	$+^{1}$
Ficus exasperata	seed			$+^{1}$	$+^{3}$	$+^{3}$	$+^{12}$
Ficus sonderi	seed					$+^{9}$	
Ficus sycomorus	seed					$+^{1}$	
Ficus sp.	seed			$+^{2}$	$+^{1}$	$+^{1}$	$+^{1}$
Grewia goetzeana	seed	$+^{1}$		$+^{3}$	$+^{1}$		
Lantana camara	seed	$+^{1}$		$+^{5}$	$+^{2}$	$+^{1}$	
Lepisanthes senegalensis	seed					$+^{1}$	$+^{8}$
Lycopersicon esculentum	seed				$+^{1}$		
Sesamum indicum	seed				$+^{1}$		
Sideroxylon inerme	seed				$+^{1}$	$+^{1}$	$+^{2}$
Solanaceae	seed			$+^{1}$	$+^{3}$		
Tamarindus indica	pod shell			$+^{1}$	$+^{1}$		
	seed residue			$+^{2}$	$+^{1}$		
Vigna membranacae	seed			$+^{1}$			

+ represents month in which eaten.
$^{1-12}$ represents number of fecal samples.

TABLE 23

Identifiable insect material in fecal samples in *Cercopithecus aethiops*, B's troop

Identifiable insect material in fecal samples	Part	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Coleoptera Curculionidae	legs			$+^{2}$		$+^{3}$	+
Hymenoptera Formicidae				$+^{1}$		$+^{2}$	$+^{5}$
Orthoptera Acrididae				$+^{2}$	$+^{1}$	$+^{5}$	$+^{3}$
Orthoptera Tettigonidae	legs				$+^{1}$		+
unidentifiable fragments				+	$+^{11}$	$+^{7}$	$+^{9}$
charcoal						$+^{4}$	$+^{4}$

+ represents month in which eaten.

$^{1-11}$ represents number of times eaten.

March. The absence in October and November was due to lack of samples from those months. Ants (*Hymenoptera Formicidae*), grasshoppers, katydids and cicadia (*Orthoptera*), and beetles (*Coleoptera*) were the most frequently found items. The great discrepancy between the data obtained from the fecal material and that from the direct observation method was not completely explicable; however, it was probably due in part to the observer's criteria for determination of a behavior as being insect consumption. In order for a behavior to be listed as insect consumption, the observer had to be able

TABLE 24

Identifiable plant material in
Cercopithecus aethiops, 2F troop, fecal samples

Identifiable plant material in fecal samples	Part	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Begonia meyeri-johni	seed	$+^{1}$	$+^{1}$	$+^{1}$	$+^{3}$		
Ficus depauperata	seed					$+^{1}$	
Ficus exasperata	seed	$+^{1}$	$+^{8}$	$+^{3}$		$+^{3}$	
Ficus populifolia	seed					$+^{3}$	
Ficus sycomorus	seed		$+^{1}$		$+^{3}$		
Grewia sp.	seed		$+^{1}$		$+^{1}$		
Lannea stuhlmanni	seed					$+^{2}$	
Lantana camara	seed	$+^{1}$	$+^{7}$		$+^{4}$		
Lycopersicon esculentum	seed		$+^{3}$		$+^{1}$		
Sideroxylon inerme	seed			$+^{1}$			
Solanaceae	seed	$+^{1}$	$+^{1}$	$+^{2}$	$+^{2}$		
Tamarindus indica	pod/seed	$+^{1}$	$+^{4}$	$+^{2}$	$+^{4}$		
Ziziphus mucronata	seed						$+^{1}$

$+$ represents the month in which eaten.
$^{1-8}$ represents the number of fecal samples.

TABLE 25

Identifiable insect material in
Cercopithecus aethiops, 2F troop, fecal samples

Identifiable insect material in fecal samples	Part	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Coleoptera Curculionidae	frag.	$+^{1}$	$+^{2}$	$+^{1}$			
Homoptera	frag.			$+^{1}$			
Hymenoptera Formicidae	frag.	$+^{1}$	$+^{2}$	$+^{2}$	$+^{1}$	$+^{1}$	
Orthoptera Acrididae	frag.		$+^{1}$	$+^{1}$	$+^{2}$		
Orthoptera Tettigonidae	frag.		$+^{1}$				
unidentifiable	frag.		$+^{6}$	$+^{1}$	$+^{2}$	$+^{2}$	

$+$ represents month in which eaten.
$^{1-6}$ represents the number of fecal samples.

to see the insect caught, held, ingest, and chewed, which was difficult due to the small size of the insect, the rapidity with which they were eaten, and the degree of scattering of the vervets themselves, which made continuous observation of all impossible. The fecal samples from the 2F troop (tables 24 and 25) were found to contain plant material that was consistent with the field observations and insect remains similar to those found in the samples from B's troop. The fragments of charcoal found in the fecal samples probably came from eating pieces of food found in the burned garbage dumps and posha discarded near hearths.

CHAPTER VII

THE BABOONS

The baboon, *Papio cynocephalus*, has one of the most extensive ranges of primates in Africa, and the habitats they occupy are equally varied. While there has been some disagreement as to the taxonomic status of the different types of baboons, it appears that all the "species" in Kenya are actually subspecies of one single species, *Papio cynocephalus* (Maples, '72). The type found at Diani is classified as *Papio cynocephalus cynocephalus*, the yellow baboon. Morphologically they appear to be long, thin baboons with markedly long limbs. The coat does not give the appearance of being as thick as the 'doguera' type and often seems unkempt and ragged. The fur is pale, and the face often has light coloration in the area of the cheeks (Maples, '72).

Considerable work has been done on the baboons in varying ecological settings, and extensive data have been amassed on their social structure, behavior, and adaptation to different ecological situations. They have most frequently been studied in the savanna habitat; this is due to the relative difficulty involved in following and observing baboons in the forest environment. The baboons seemed to be exceedingly well adapted to terrestrial habitat, requiring trees and other elevated refuges, such as cliffs, only for sleeping. Thus, in the forest, they usually move on the ground preferring areas of thick underbrush cover, which are relatively impenetrable by humans.

At Diani, the situation as it existed during the course of the investigation was poor for gathering data on the baboons. The baboons tended to use the forest for refuge and to some extent for food. When they left the forest, they usually moved into secondary growth areas which often were predominantly thickets or fields of *Lantana camara*, which were most difficult to traverse. Since the baboons were notorious crop raiders, they were almost uniformly disliked by the European and African people. They were constantly blamed for destruction of coconut, papaya, and mango crops and considered a pest worthy of the most severe retaliation. Every opportunity was taken by the local people to harass them. The situation was further complicated by the fact that most of the study was done during the dry season; it was possible that baboon utilization of this area was less during this time than during other seasons. No natural source of water was seen in the study area or forest proper. The baboons were only seen drinking water on a few occasions; each time they obtained water from the faucets at the Two Fishes Hotel's water cistern in the forest.

Two troops of baboons were found to use the Diani Forest. The large troop, the Cotton Shamba troop, was found at the most southern edge of the forest, and the smaller troop, the Jadini troop, ranged from south of Coverdale's northward to beyond the Jadini Hotel (fig. 22). The Cotton Shamba troop, of which 50 individuals were counted, was much larger than the Jadini troop of 11 members. The two troops were seen simultaneously on two occasions, February 8, 1973, and February 9, 1973. No antagonism was seen between the troops on the highway, but the forest had become unusually noisy with baboon screaming prior to their arrival on the highway.

The baboons were observed on only 25 days during the study period, usually for less than a few hours. Dietary information was gathered mainly on the Jadini troop, though plant and fecal samples were also collected from the Cotton Shamba troop. The investigator systematically looked for them for a period of three to four days each month and, also, tried to pick them up whenever they were sighted while observing a different species. This, however, was done less frequently if they were sighted while following the sykes since they, also, were difficult to follow and habituate. The baboons, despite their position

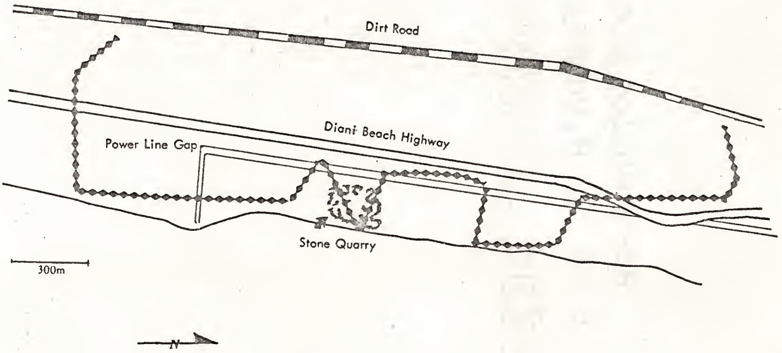


Fig. 22 Range of *Papio cynocephalus*, Jadini troop, in relation to the study site.

as vermin, were not shy and could be watched at relatively close distances. They did not tolerate continuous observation, however, frequently threatening the observer or retiring to inaccessible scrub areas.

When the baboons were in the Diani Forest, they tended to utilize the highway or the old dirt road and other transects for traveling. In October and November, they were usually seen in the southern part of the forest; after that, they utilized the northern part more, coming into the study site at Bonham's Forest and the Jadini Hotel area.

One sleeping area, a section of the forest west of the highway, was seen to be used several times. Most of their resting occurred during the late morning in the forest or thickets, and it was usually at this point that they were lost either for the day or, occasionally, until they showed up again in the late afternoon. On those occasions, when they were observed resting, they utilized both the ground and the trees. Play behavior was observed on the ground and in low shrubs more than in trees. Foraging was predominantly observed on the ground, often on the sides of the highway in disturbed growth; however, trees were also utilized, especially for fruits as they were in season.

It was realized that the plants observed being eaten by the baboons probably constituted only a small portion of the total number of plant species consumed, because the the baboons were infrequently observed, and possibly the

TABLE 26

Plants observed eaten by *Papio cynocephalus*

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Adansonia digitata	flower/ fruit	+					+
Combretum schumannii	seed			+			
**Eragrostis ciliaris*	blade/root						
**Eragrostis sp.*	blade/root						+
**Euphorbia hirsuita*	blade/root					+	
Fernandoa magnifera	flower					+	
Ficus exasperata	fruit		+				+
Ficus sycomorus	fruit					+	
Ficus sp. #117	root					+	
Ficus sp. #118	root						+
**Gramineae*	blade/root					+	
**Hyphaene coriacea*	fruit						+
**Lantana camara*	seed		+				
**Leptochloa obtusiflora*	blade/root			+			
**Mariscus dubius*	blade/root			+			
**Ricinus communis*							
Sideroxylon inerme	uk	+					
Tamarindus indica	fruit		+				
Cultigens:							
Ananas comosus (pineapple)	fruit						+
Carica papaya (papaya)	fruit						+
Cocos nucifera (coconut)	fruit					+	+
Mangifera indica (mango)							+

+ represents month in which eaten.
* represents secondary association.

TABLE 27

Identifiable plant material in
Papio cynocephalus fecal samples

Identifiable plant material in fecal samples	Part	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Eleusine indica	seed				$+^1$		$+^1$
Eragrostis sp.	seed				$+^1$		
Ficus depauperata	seed		$+^1$				
Ficus exasperata	seed		$+^1$			$+^2$	$+^1$
Ficus populifolia	seed		$+^1$				
Ficus sycomorus	seed		$+^2$			$+^2$	$+^1$
Ficus sp.	seed					$+^1$	$+^1$
Lantana camara	seed	$+^1$	$+^6$		$+^1$	$+^7$	
Solanaceae	seed	$+^1$	$+^1$				
Tamarindus indica	pod/ frag.		$+^1$		$+^1$		
grass (not indentified)	seed/inflo-resence		$+^1$		$+^2$		$+^3$
Cultigens:							
Carica papaya (papaya)	seed					$+^1$	
Cucumis sativus (cucumber)	seed				$+^1$		
Cucurbitaceae	seed					$+^1$	
Lycopersicon esculentum	seed					$+^1$	
Sesamum indicum	seed		$+^1$		$+^1$		

+ represents month in which eaten.
$^{1-7}$ represents number of fecal samples.

TABLE 28

Identifiable insect material in
Papio cynocephalus fecal samples

Identifiable insect material in fecal samples	Part	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Coleoptera	frag.		$+^{2}$				
Hemiptera Pentomidae	frag.		$+^{2}$				
Hymenoptera Formicidae	frag.	$+^{1}$	$+^{1}$		$+^{1}$	$+^{1}$	$+^{1}$
Neuroptera Asculaphidae	mandible					$+^{1}$	
Orthoptera Acrididae	frag.					$+^{2}$	$+^{1}$
Orthoptera Phasmidae	frag.					$+^{1}$	
Orthoptera Gryllidae	frag.		$+^{1}$				
Orthoptera Tettigonidae	frag.				$+^{1}$		$+^{1}$
unidentifiable	frag.		$+^{3}$		$+^{2}$	$+^{5}$	$+^{1}$

+ represents the month in which eaten.
$^{1-5}$ represents the number of fecal samples.

Diani Forest was only a section of a larger range which was never determined. The 25 plants observed eaten are listed in table 26. Of the cultigens, only the coconut *(Cocos mucifera)* was seen taken from trees; these were usually unripe and were shredded with the canines; and, the liquid and pulp, if any were present, were consumed. (Only adults were observed eating coconuts in this manner.) The other cultigens were eaten from garbage dumps; as indicated previously, the baboons were reported to raid these and crops. Different species of figs and grasses were predominant components of the diet; both were available throughout the year and, coupled with *Lantana camara* seeds, probably contituted the most important items gleaned from the area.

The fecal analysis amplified data on observed food items and also revealed four additional cultigens that were eaten (table 27): *Cucumis sativus* (cucumber), *Cucurbitaceae* (common name unknown), *Lycopersicon esculentum* (tomato), and *Sesamum indicum* (sesame); it was never determined where or how these were obtained. No instance of insect or vertebrate material were observed being eaten, although there were insect remains in the fecal samples (table 28).

CHAPTER VIII

INTERSPECIFIC ASSOCIATIONS AND INTERACTIONS

Within the context of the project, interspecific interactions were seen to occur on numerous occasions. The study site contained four troops of different species whose ranges overlapped; thus, the probability that they would come into contact was increased. Table 29 shows the frequency of the different types of associations that

TABLE 29

Single species and polyspecific associations

Month	C+S	C+V	C+B	S+V	S+B	V+B	C+ S+V	C+ S+B	V+ S+B	C+V S+B	C	S	V	B
October	2	3			1		1				2		1	4
November	11	3	1	2			2				2	1	1	2
December	17	1	2	3	2		1					2		6
January	5			2	1		1				2	2	2	
February	13		1	4			1		1		2	1		2
March	13			9							1	1		3

C represents the colobus.
B represents the baboon.
S represents the sykes.
V represents the vervet.

occurred during the investigation. An association was noted as such when the individuals of two or more species were in proximity according to definition by Gartlan and Struhsaker:

> Two or more species are said to be in association when members of the different species are in such proximity that members of one species are often interposed between conspecifics of another. ('72:233-234)

An association was only recorded once if it remained the same, even for a long time period. If another species entered the area after the association had been stable for one-half hour or more, it was considered terminated, and a new association of three species was noted. If an association disbanded because either or both species moved, it was considered terminated. If the two troops involved moved separately, i.e., not as a mixed group, but reformed in a new site, it was scored as a new association. When a single species was followed on one day and did not form any associations, it was only scored once. Individual sightings of a troop that occurred when they were not being studied intensively were not scored since the context in which they occurred was not known. Thus, the chart gives no indication as to the length of an association or the social factors involved, but does indicate the frequency and consistency with which associations occurred.

Colobus and Sykes Interactions

The colobus and sykes were seen in association more frequently than any other combination of two or more species. The majority of associations were pacific or neutral (fig. 23). No special behaviors were seen at the formation or termination of the associations, and usually no interactions occurred either between individuals or the whole troop. These situations occurred while either one or both of the species were eating, even in the same tree, and while they were sitting quietly at rest. For the most part, the arrival of one did not disrupt the activities of the other. On six occasions, a colobus was seen to displace a sykes, but sykes were never seen displacing colobus; on one of these occurrences, the displaced sykes returned and swatted the colobus' tail, but this did not elicit any response from the colobus. They were never seen to groom one another. It is possible that juveniles played with each other on several occasions, but it was always too difficult to actually see what was happening. On only one occasion did the colobus respond to the vocalizations of the sykes; the sykes had been vocalizing at the investigator, and the colobus moved into higher branches. If at any other time the colobus responded to the vocalizations of the sykes, the behavior was too indistinct to be recorded as such. They were never seen to travel together as a mixed group; although on two occasions, the troops moved in the

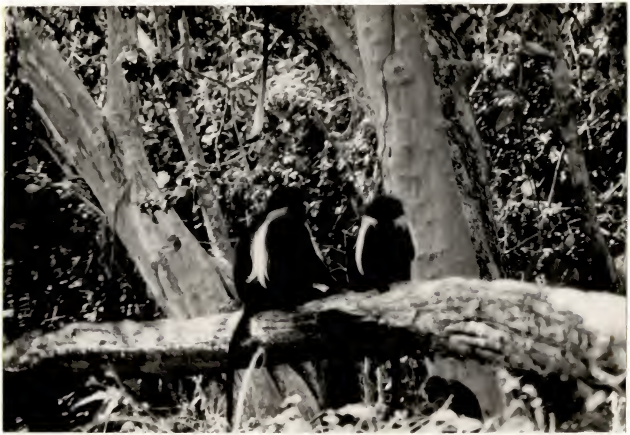


Fig. 23 A typical association between *Colobus angolensis* and *Cercopithecus mitis*.

same direction at the same time, but separate troop integrity was maintained.

During February and March, a slight shift in the timing of feeding resulted in different interactions. At this time, the colobus were seen eating buds and leaves from a particular tamarind tree with only one or two sykes present. After the colobus stopped eating, more sykes entered the tree and began feeding. The colobus remained resting in the tree, undisturbed by the sykes' presence. This pattern was not noticed in relation to other food items or for tamarind pods which were eaten in November and December. The colobus, however, did not eat the tamarind pods as consistently or in the same quantity as they ate the buds and leaves.

Sykes and Vervet Interactions

The interactions and associations between the sykes and the vervets were less frequent and appeared to be more aggressive. On one occasion (November 4, 1972), loud vocalizations from the area of a fruiting tamarind tree in the southeastern part of Bonham's Forest were heard. The sykes appeared to be dispersed in the area, and some of them were seen chasing an adult vervet. The vocalizations and the interaction lasted for 21 minutes and ended with the departure of the vervet. It was not known if other vervets had been present, but the vervet troop was seen in the area later that day. On November 22, 1972, the sykes and vervets were seen together at the same tamarind tree. The vervets arrived first; when the sykes moved in to the tree, the vervets began moving around more frequently. Vervets were seen displacing the sykes twice and chasing them three times; on one occasion this resulted in a sykes displacing another sykes. The vervets were displaced by the sykes twice. After 20 minutes they appeared to settle down; the vervets concentrated their feeding on the south side of the tree and the sykes on the north side. One hour and 50 minutes later, the two troops were seen in the coral outcrop area at Bonham's; there were no interactions, even when they were seen sitting next to each other.

In January, no antagonism was seen when they fed together, and in February and March, the vervets were not eating in the same area as the sykes troop. The vervets, however, were seen in association with members of a different sykes troop in the area of the Jadini and Wells. On two occasions, while feeding with this troop, a sykes was seen to displace a vervet; an adult female vervet with an infant was displaced, and on a different occasion an adult male vervet was displaced. Both interactions took place while they were feeding on *Lepisanthes senegalensis*. On other occasions, the vervets were seen feeding in the more terminal branches or in different trees, and no interactions occurred. Usually, however, when behavior associated with mixed feeding was neutral, only one or two sykes were present; more sykes were seen during aggressive interactions.

On one occasion, a juvenile sykes was seen to groom a juvenile vervet; however, the vervet did not reciprocate. The vervets were observed once to respond to the chirping of the sykes as the investigator approached them. They did not flee, but merely moved from the ground to some nearby branches. Twice young vervets were seen to show interest in sykes as they passed, by either swatting the sykes' tail or following the animal; this did not elicit any behavior from the sykes involved.

Colobus and Vervet Interactions

The colobus and vervets were only seen together in a two-species association during the months of October, November, and December. In October, they were seen resting in the coral outcrop area at Bonham's three times; no interactions were recorded. During November, two neutral associations were seen in the coral outcrop area. In the fruiting tamarind tree in the southeastern part of the forest, displacement activity was seen once during an association; a vervet who had just been displaced by a colobus was seen displacing another colobus; and then two colobus were seen chasing a vervet. In December, a colobus was again seen chasing and displacing a vervet.

Baboon Interactions with Other Species

On all four occasions when colobus and baboons were seen together, there were no interactions between them. The investigator's arrival sometimes caused the baboons to leave, thus terminating the association; otherwise, they continued resting as they were. The two times baboons were seen with sykes in the study area, it appeared as though the baboon's arrival caused the sykes to leave; this was seen to happen while the sykes were feeding in tamarind trees, once in December and once in January. The baboons arrived silently, and almost simultaneously the sykes were seen leaving. A similar event happened in February as a sykes was sitting in some bushes with the vervet troop at the northern edge of Bonham's Forest, near the Jadini. They quietly receded into the bushes and then the baboons were seen approaching from the northwest. The baboons were also seen chasing a group of vocalizing sykes on the southern edge of the Diani Forest, but this did not involve the troops from the main study site. Thus, there was little interaction or association between the baboons and the other species. Baboons have been known to kill and eat vervets in other areas, but it was not known if that ever happened at Diani, nor was it known if they killed and ate any of the other species present.

Colobus, Sykes, and Vervet Interactions

Only one association of the three species led to displacement and threat behavior. On November 30, 1972, the colobus, sykes, and vervets were seen together in and around the tamarind tree in the southeastern part of Bonham's Forest. After two sykes were displaced by the vervets, a colobus jumped into the tamarind tree and displaced a vervet. Shortly afterwards, a vervet was seen threatening a colobus; the colobus subsequently moved to a lower branch. At other times, when they were seen together in the forest or the coral outcrop, associations were loose and neutral.

Comments

In looking at interspecific associations in the context of this study, it can be seen that as Groves noted, "it seems that the local conditions rather than the species themselves may be the deciding factor in their [polyspecific associations] formation " ('73:21). The data indicate that within the boundaries of the study site, which has ultimately been defined by the ranges of the four species, it was the interplay of the distribution of resources and the specific responses of the individual species to the resources that largely influenced the type and frequency of the associations. However, the phylogenetic histories of the species cannot be ignored in the interpretation of the data, especially since congeneric species associations were characterized by a higher level of aggressive behavior, particularly in concurrent feeding situations; they were also the only situations in which interspecific grooming was seen. The evidence was not conclusive, but it appeared that the interactions were more affected by the taxonomic status of the species involved, while the frequency and type of association were more related to the local ecological conditions.

CHAPTER IX

RESULTS AND DISCUSSION

Results

The Diani Beach forest provided a suitable habitat for four species of cercopithecoid primates: one in the subfamily *Colobinae*, *Colobus angolensis palliatus*, and three in the subfamily *Cercopithecinae*; of these *Cercopithecinae*, two were in the same genus *Cercopithecus*, *C. aethiops* and *C. mitis*, one in the genus *Papio*. Thus, varying degrees of taxonomic relatedness were expressed. Given the degrees of morphological, biological, and behavioral differences found in such a primate population, it was expected that differences in resource utilization would result in habitat partitioning effective enough in all cases to reduce interspecific competition to minimum levels. In studying the associations and interactions which occurred during the course of the investigation, it was found that most were neutral or peaceful, even in feeding situations. While all the nuances of ecological adaptation and niche measurement were unattainable in the scope of this study, it was found that the species were utilizing the habitat differentially, and partitioning could be seen in terms of both species range and diet.

Spatial Utilization

The movement of the four species during the course of the investigation showed seasonal variation in the utilization of the main sector of primary forest remnant in the study site. The wet season, during the short rains of October, November, and early December, was marked by the presence of the colobus and sykes troops, frequent visits by the vervets, and only occasional sightings of the baboons. This pattern shifted during the dry season of mid-December through the end of March so that the sykes were utilizing the southern end of the study site to a high degree, although still ranging into and utilizing Bonham's Forest; the vervets shifted to a more concentrated use of the northern part of the study site and virtually ceased going into the forest. The occurrence of the baboons increased during this period, and the colobus remained virtually the same.

Figure 24 illustrates the maximum range overlap of the four species at the study site during the course of the investigation. The colobus range was the smallest and the others, in order of increasing size, sykes, vervets, and baboons, overlapped each other predominantly in the area that was used most intensively by the colobus.

Vertical separation was not as clear cut. The colobus were the most arboreal of the four species, feeding, resting, sleeping, and moving in the trees. They tended to

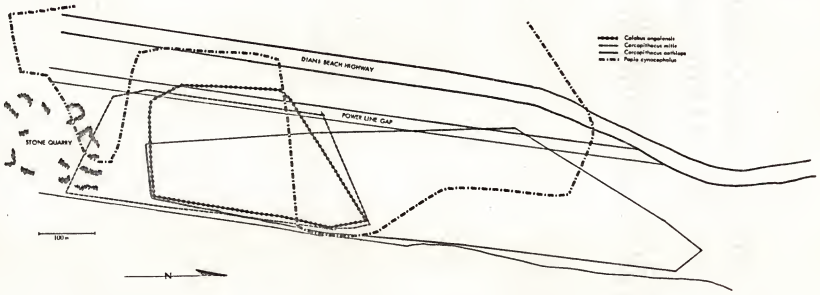


Fig. 24 Overlap in the maximum ranges of the four species at the study site, November, 1972 - March, 1973.

prefer the upper canopy, but could frequently be seen feeding in the lower story of bushes and shrubs. They were least seen on or near the ground, though they did eat and move on the ground and, occasionally, were seen sitting on fallen trees or stumps.

The sykes monkey was midway between the arboreal colobus and the more terrestrial vervets and baboons in this particular area. They were seen moving on the ground in cleared areas and in the forest. Feeding and resting occurred on the ground and in the trees. They preferred the upper canopy and rarely sat or fed in bushes, shrubs, or small trees. Both the colobus and the sykes were frequently seen leaping from one tree to another and, occasionally, these jumps resulted in falls.

The vervets traveled more frequently on the ground than in the trees and were not seen attempting to bridge wide gaps between trees; their arboreal pathways most often were by means of interconnecting branches. They, also, fed on the ground and in the trees, frequently taking their food into a tree, presumably for greater safety from humans and other vervets. When the whole troop rested together in a localized resting site, they always stayed in the trees; individuals, however, occasionally sat around resting on the ground or on boulders.

The distribution of major resting sites (fig. 25) and feeding sites (fig. 26) for the sykes, vervets, and colobus followed a pattern similar to that of their ranges. There

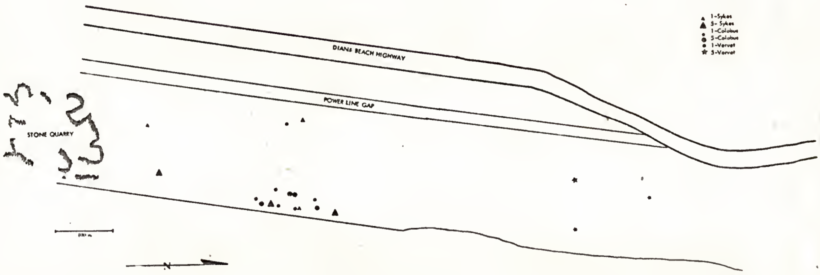


Fig. 25 Distribution of commonly'used resting sites of the three species at the study site, November, 1972 - March, 1973.

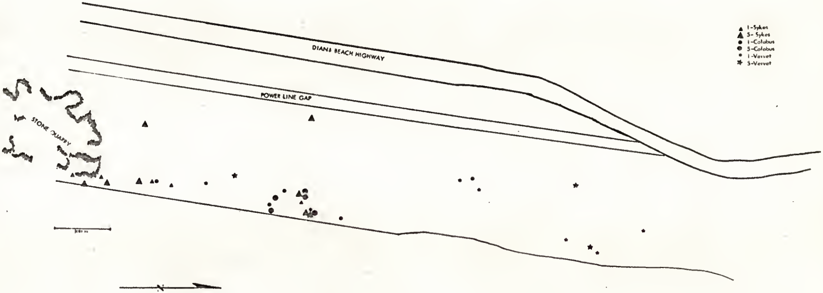


Fig. 26 Distribution of feeding sites of the three species at the study site, November, 1972 - March, 1973.

was some overlap and clustering in the area of the coral outcrop and southeastern part of the forest coinciding with the areas used most heavily by the colobus; but the sykes also used the southern area, and the vervets the north. The baboons were seen raiding coconut trees that grew near the beach between the Jadini Hotel and Bonham's on several occasions. They were also found in the area of the tamarind trees in the southeastern and southwestern sections of Bonham's Forest, but were never actually seen eating there. The baboons were frequently observed feeding at the highway shoulders, the Jadini Hotel garbage dump, and the yard of a house west of the Two Fishes Hotel. They were also seen sitting quietly in the midafternoon in the forest south of Coverdale's property and west of the power lines, as well as west of the highway between the Jadini Hotel and Two Fishes Hotel intersections.

Differential Diet

The nature of the Diani Beach area, with its small stands of primary forest, interspersed human habitation sites, and agricultural plots, provided a very nonhomogeneous and diversified habitat. Years of cutting in the forest permitted the growth and spread of secondary bush, and the relatively high density of human recreational accomodations had introduced ornamental plants, plots of cultigens, and garbage dumps. In adapting to such an environment, some of the primates have taken advantage of what might be considered a negative situation; in fact, it was the relative proportions of primary, secondary, and introduced food items that was seen as one of the areas of major importance in partitioning.

In classifying the types of plants in the study site, the investigator considered all trees and shrubs that grew in untouched parts of Bonham's Forest as primary association. Others that grew in the more disturbed areas were considered as part of the primary association if they were indicated as growing in the coast province in Dale and Greenway ('61) or noted as part of type IV forest by Moomaw ('60). Plants, especially vines, shrubs, grasses, and what appeared to be weeds, were included in the list of secondary flora as in Moomaw ('60). Plants that were conspicuously placed around houses and hotels, particularly if they were in flower or fruit, were considered ornamentals and checked in Bailey's ('49) manual of cultivated plants and Dale and Greenway ('61). The cultigens were easily recognizable as such.

Of the 34 plants classified as primary association (table 30), only four were eaten by all four species: *Ficus exasperata*, *Ficus sycomorous*, *Sideroxylon inerme*, and the fruit of *Tamarindus indica*; of these, only *Tamarindus indica* was eaten by all four in the same month. None of the secondary (table 31) or introduced cultigen (tables 32 and 33) groups were eaten by all four species.

TABLE 30

Comparison of "primary association" plants eaten by the four primate species. Composite chart from observed data and fecal analysis.

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Adansonia digitata	leaf				C°		
	bud				C	C	C
	bud case					S	S
	flower					C	CB
	fruit	B				C	C
Afzelia quanensis	leaf						C
Capparis tomentosa	leaf						C
Carpodiptera africana	leaf		V				
Combretum schumannii	seed		C	B			
Dalbergia melanoxylon	seed	SV	V	S			
Drypetes gerrardii	leaf		C	C	C	C	
Drypetes natalensis	fruit				V		
Fernandoa magnifica	flower					B°	
Ficus depauperata	fruit		VB	V		V	V
Ficus exasperata	fruit		B	CV	V	SVB	SVB
Ficus populifolia	fruit		B				CS
Ficus sansibarica	leaf		C	C			
Ficus sonderi	fruit				S	V	
Ficus sycomorus	fruit		B	V	V	SVB	CB
Ficus sp. (2 species)	root					B	
Ficus sp. (4 species)	leaf			C	C	C	C
Haplocoeum inoploeum	leaf	C	C	C	C		
Lannea stuhlmannii	fruit/seed				VS		VS
	leaf stem				V		V
Lecaniodiscus fraxinifolius	fruit		S°		S		
Lepisanthes senegalensis	fruit					CV	CSV
Manilkara sansibarensis	fruit				S		

Table 30 (continued)

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Meliaceae	leaf		C				
Monanthotaxis fornicata	leaf					C	
Rhamnaceae	leaf		C	C	C		
Rutaceae	leaf	C	C				
Sideroxylon inerme	seed	B	CV	CS	CSV	SV	CSV
Stadmannia sideroxylon	seed				CS	C	
Suregada zanzibarensis						S	S
Tamarindus indica	bud			C		CS	CS
	leaf					CS	CS
	fruit		CSVB	CSV	CSVB	S	
Tarenna nigrescens	leaf					C°	
Thunbergia holstii		V					
Trichilia roka	leaf						C
Ziziphus mucronata	fruit					S	S

B represents eaten by baboon.
C represents eaten by colobus.
S represents eaten by sykes.
V represents eaten by vervet. (2F troop is not included.)
° represents the possibility of being eaten.

TABLE 31

Comparison of "secondary association" plants eaten by the four primate species. Composite chart from observed data and fecal analysis.

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Abutilon mauritianium	flower		V	V	V		
	bud		V	V	V		
	seed		V	V	V		
Alysicarpus rugosius						V	
Begonia meryeri-johni	fruit	CS			V		
Cissus rotundifolia	leaf				S		
Cynanchum sp.	leaf		C	C			
Cyphostemma adenocaule	leaf		C	C			
Elusine indica	seed				B		B
Eragrostis sp.	grass blade				B		B
Euphorbia hirsuita	blade/root					B	
Gramineae	blade/root					B	
Grewia goetzeana	fruit	V		SV	SV		
Hoslundia opposita	leaf	V°		C			
Hyphaene coriacea	fruit						SB
Jasminum abyssinicum	leaf				V		
Lablab sp.	flower/seed			V	V		V
Lantana camara	seed	VB	B	SV	SVB	VB	
Leptochloa obtusiflora	blade/root			B			
Mariscus dubius	blade/root			B			
Phyllanthus sp.	fruit					V	
Premna hildebrandtii	leaf		C				
Pseuderanthemum hildebrandtii	flower		S	S	SV		
Ricinus communis		B					
Securinega virosa	seed					V	
Solanacae		B	B	V	V		
Vigna membraceace			V	V	V		

B represents eaten by the baboon; C, the colobus; S, the sykes; V, the vervet (2F troop not included); ° represents the possibility of being eaten.

TABLE 32

Comparison of ornamental plants and cultigens eaten by four primate species. Composite chart from observed data and fecal analysis.

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Annona squamosa	fruit		V	V	V	S	
Annona reticulata	bud		S				
Averrhoa carambola	fruit				V		
Azadirachta indica	fruit					V	V
Bougainvillea spectabilis	pulp		V		V	V	V
Caesalpinia pulcherrima	seed	V		V	SV	V	
Carica papaya	leaf/fruit						V
Chrysophyllum cainito	fruit					S	SV
Cocos nucifera	fruit/pulp					B	B
Delonix regia	seed	V					
Lycopersicon esculentum	fruit	V	V		V		
Manilkara obovata	fruit			SV	S		
Manilkara zapota	fruit					V	V
Musa sp.	fruit					V	V
Pandanus (?kirkii)	fruit		V				
Psidium guava	fruit	V		V	V	V	

B represents eaten by the baboon.
S represents eaten by the sykes.
V represents eaten by the vervet. (The 2F troop is not included.)

TABLE 33

Comparison of cultigens obtained from unstable (garbage dumps, fed by humans) and unknown sources (probably raids). Composite chart from observed data and fecal samples.

Plant eaten	Part eaten	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Ananas comosus	fruit		V	V	V	V	VB
Carica papaya	fruit			SV	V	VB	VB
Citrus limon	fruit	V					
Citrus paradisia	fruit				V	V	
Citrus sinensis	fruit					V	V
Cocos nucifera	pulp/fruit				V	V	V
Cucumis sativus	fruit				B		
Cucurbitaceae	seed					B	
Daucus carota	root					V	
Mangifera indica	fruit		V				VB
Sesamum indicum	seed		B		V	B	

B represents eaten by baboon.
S represents eaten by sykes.
V represents eaten by vervet. (The 2F troop is not included.)

The colobus, sykes, and vervets ate the fruit of two items in common: *Lepisanthes senegalensis* (primary association) and *Begonia meyeri-johni* (secondary association). The colobus, sykes, and baboon ate two items in common: *Adansonia digitata* and one Ficus species (both from the primary association). The seeds of *Lantana camara* were eaten by the vervet, sykes, and baboon. This secondary plant was so rampant in the area, it is unlikely that there was any competition for it. Eight plants, four ornamental/ cultigen, two secondary and two primary, were eaten by both the sykes and vervets. The vervets, colobus, and sykes each ate one item in common with the baboon; the sykes and colobus shared two, both from the primary association; and, the colobus and vervets possibly one. It is seen that, in actuality, only a small number of the total plants known to be eaten by the four troops in the study site were shared. The greatest overlap was observed between the sykes and the other species.

Those items which were eaten exclusively by each species are indicative of what can be considered the specialization or route of adaptation of each species. The colobus ate 15 items exclusively; 13 were members of the primary association and, in all cases, only the leaves were eaten. In light of what is known of the *Colobinae*, as to the specializations of their gastrointestinal tract and digestive processes, this was not surprising. Obviously, they ate fruits, seeds, and insects, but they were adapted for a specialization of leaf eating, which was not found in any of the other three species. They were seen to differ in their feeding behavior patterns, which was characterized by casual feeding interspersed between two main intensive feeding periods. This was possibly related to the digestive process necessary for foliage and the relatively large quantities of leaves necessary to maintain the animal.

Only six of 24 items were eaten exclusively by the sykes. While they shared a considerable percentage of their dietary constituents, they showed a marked reliance on a few staple items which appeared to be in abundance in the habitat. This type of focal feeding seemingly has had wide ranging effects on the dispersion patterns seen in this species, both during feeding and movement. The most important items were *Tamarindus indica, Sideroxylon inerme,* and possibly the figs. These items were eaten most consistently throughout the study; but of these, *Tamarindus indica* was the predominant item eaten, the fruit, flowers, and leaves being consumed at various times. The diet was supplemented with seasonal items, particularly when tamarind fruit was scarce or unavailable. Through a pattern of high troop dispersal, while feeding on seasonal items which were spaced in the habitat or not in abundance, they effectively reduced intratroop and interspecific competition for these items; at these times, small mixed groups and single adult males were seen dispersed in the area. However, when a single item was in fruit or flower so that it was an abundant or superabundant item, troop dispersion was reduced, and the troop converged about this item, thereby effectively utilizing it to a maximum. It is this pattern then which apparently provided a partitioning mechanism for the *C. mitis* population.

The vervets were characterized by their high reliance on the secondary association and ornamental/cultigen group. Of the total 47 items they were seen to eat, only 11 came from the primary association. They primarily ate fruits and seeds. Eighteen items were eaten only by the vervets; six from the secondary association, eight from the ornamental/cultigen group, and four from the primary association. The vervets concentrated on the secondary association and ornamental/cultigens as resources rather than the primary association. They also were characterized by a high degree of daily variety. Feeding activity occurred throughout the day rather than at marked intervals; this pattern was probably further reinforced by sporadic feeding by tourists at the hotels and houses. Consequently, the vervets were highly adaptive primates showing versatility in exploiting environmental conditions. Flexibility in response to ecotonal and marginal habitats was obtained by maintaining an omnivorous diet, some relaxation of daily rhythms and generalized anatomy. Adaptability, the vervets means of success, provided an effective way of reducing competition. The apparent phylogenetic pattern of a dispersed troop, especially during feeding periods, has been adapted to a niche of scattered, relatively nonabundant, and sometimes unstable resources which, when utilized to a maximum, provided an adequate diet.

For the period represented by the investigation, the baboons utilized the study site minimally and did not appear to display much dietary overlap with the other species. Ten items out of their total of 25 were exclusive, and seven of these were grasses. They ate cultigens such as sesame, cucumber, tomato, coconut, and papaya, which they procured by raiding shambas (farms) since they were not fed by the people in the area. The use of grass is characteristic of baboons elsewhere, and these items were not eaten by any other of the primates at Diani. This grass utilization is particularly characteristic of baboons in the savanna habitat and provides a successful adaptation for them in that environment. At Diani, a disturbed forest, the baboon population through continued reliance on this resource and exploitation of human agricultural products reduced interspecific competition.

The results of an analysis of variance of the proportion of insect material in the fecal samples (Appendix) indicated that there was no significant difference in the amount of insect remains in the feces for the vervets, sykes, and baboons in the wet or dry seasons encompassed in this investigation. The results further indicated that the data collected showed as much variation on a troop basis as it did on a species basis. The colobus, however, ate markedly less insect material and were not considered in the analysis. Furthermore, the types of insects identified in the samples from the species did not differ to any extent. Consequently, it was concluded that for the period of the study, the insect component of the diet did not significantly contribute toward effective resource partitioning.

Discussion

The data obtained in this study contributed toward an understanding of the need to expand the traditional methods used in investigating primate ecology, in general, and the relationship between ecology and social structure. Feral primates usually require a period of habituation to the observer's presence before adequate conditions for monitoring their behavior can be attained. The more arboreal species often remain screened from view by dense foliage. Thus, continuous observations are not possible under these conditions, and it becomes necessary to amplify field observations to as great an extent as possible. The use of the technique of collecting and analyzing fecal samples is seen as one possible method for obtaining more information on primate diets.

The combination of direct field observation and fecal analysis in this study resulted in a more complete understanding of the plant and insect components of the diets of the species studied. It also provided more information on the time periods during which the items were being consumed. It is felt that further refinement of this technique and the quantification of such data will lead to a better understanding of primate diets and the differences that exist over a period of time for individual troops, as well as between troops and among species.

Secondly, it can be seen that in attempting to understand the relationship between primate social organization and ecological position, the allocation of species to environmental "grades", such as forest, forest fringe, tree savanna, or grassland, is not entirely adequate (Crook and Gartlan, '66; Crook, '70). The distinction must be made between habitat, or the place where an organism lives, and its niche, the inclusive term for the physical space occupied by an organism, its functional role in a community, and its position in the environmental gradients of temperature, moisture, and other conditions of existence (Odum, '71). It is only at the level of the niche that one can begin to extract meaningful information about the placement and interrelationship of species in the natural system and community. It is not sufficient to merely describe the ecological situation in which a species is found, but an attempt must be made to perceive it in terms of all the interrelated processes that it enters into in fulfilling its requirements for survival and the biological role it occupies in nature. In addition to these variables, it also becomes necessary to consider the evolutionary history of the species, i.e., its phylogeny.

Furthermore, the study of sympatric populations, such as at Diani Beach, permits direct comparison of arboreal and terrestrial species. It is seen that the baboons and vervets have wider ranges of exploitative means than the colobus or sykes; but even the most restricted, the colobus, maintain some degree of variability in their diet. The sykes, vervets, and baboons show a trend toward a greater degree of diversification in terms of number of items and variety of items consumed. Thus, in relying less on the stable, more homogeneous nature of the arboreal niche, the more terrestrial forms have increasingly adapted to unstable, heterogeneous habitats requiring the ability to respond quickly to daily and seasonal fluctuations. Studies of the autecology and synecology of primates will hopefully lead to a better understanding of the relationship between behavior and ecology and the patterns of adaptation within the primate order.

CHAPTER X

SUMMARY

The faunal assemblage of a small coastal forest in Kenya was found to include a primate population containing one *Colobinae*, *Colobus angolensis palliatus*, and three *Cercopithecinae*, two in the genus *Cercopitheus*, *C. aethiops* and *C. mitis*, and one in the genus *Papio*, *Papio cynocephalus cynocephalus*. Polyspecific associations were found composed of various combinations of all four species, but never more than three species were found together at a time. Interactions within these associations were usually pacific or neutral; aggressive interactions usually involved the presence of the two *Cercopitheus* species; also, the only occurrence of interspecific grooming occurred between two juveniles of *C. mitis* and *C. aethiops*.

The observation of these various associations and interactions lead to the hypothesis that the forest habitat offered enough variety so that some means of partitioning reduced competition among the primate species. Since primates spend a large amount of time in feeding activity, and because it is often stated that partitioning is resource-related, attention was focused on the diets and space-use patterns of the primates. Observational data on the dietary habits were supplemented by a collection of fecal samples which were analyzed for identifiable food remains. A study site which was used by all four species was selected for the investigation.

It was found that the ranges of the species varied considerably in the sykes, vervets, and baboons, while to a lesser extent for the colobus. Vertical utilization of the study site overlapped considerably, but some species differences in movement routes, resting places, and feeding sites did exist. The colobus were the most arboreal and the baboons the most terrestrial. The sykes and vervets appeared equally at home in both, but the vervets were the more terrestrial of the two.

A total of 76 plants were collected by observing what was eaten in the field. Dietary information was greatly amplified by the use of fecal analysis, especially for obtaining information on the insect component of the diet, as well as items which were eaten in the dense foliage out of view of the observer.

Some degree of overlap in diet was found to exist among all the primate species. Each, however, can be seen to be utilizing the habitat differentially. The colobus, while eating seeds, fruits, and buds, relied heavily on a diet composed of a high percentage of leaves not eaten by any of the other species. The sykes were seen as "focal feeders," adapting through a pattern of eating a few items, mainly *Tamarindus indica*, throughout the term of the project and supplementing this with seasonal items. This pattern had apparently affected their social structure and behavior considerably. The vervets were most closely tied to the forest fringe, relying heavily on secondary association plants, ornamental trees, cultigens, handouts from people, and leftovers in garbage piles. The baboons followed a similar pattern, but had a much wider range, utilizing the forest to a lesser degree and mainly as a refuge for sleeping. They also obtained some of their food from raiding local farms and foraging through garbage piles. They were seen to be differentiated through their comsumption of a number of grasses which were not eaten by any of the other species.

APPENDIX

FECAL SAMPLES AND ANALYSIS

APPENDIX

The fecal samples collected during this project were dried and macrosorted. The results (table 34) were compared qualitatively and are included in the preceding chapters. One of the important findings from their analysis was that considerably more insect material was found in the fecal material than was expected from the data gathered in the field observations. Literature on diets of feral primates indicate that many species eat insects (Altmann and Altmann, '70; Chance and Jolly, '70; Jones, '72; Thorington, '67). It was found that all the species in this investigation, colobus included, had consumed and digested some insect material. The amount eaten by the colobus, however, was minimal and was not considered in the statistical analysis discussed here.

The objective of the analysis was to determine whether there was any significant difference in the amount of identifiable insect remains among the vervets, sykes, and baboons. If the differences found were significant, it could be possible that the insect component of the diet was contributing toward effective resource partitioning.

In order to compensate for differences in the weights of the samples, the proportion of the weight of the insect material to the total weight of the sample (sample weight

TABLE 34

Identifiable items in fecal samples

Sample #	Species	Total dry weight - g.	*Azadirachta indica*	*Begonia meyeri-johni*	*Carica papaya*	*Cucumis sativus*	*Elusine sp.*	*Eragrostis sp.*	*Ficus depauperata*	*Ficus exasperata*	*Ficus sonderi*	*Ficus sycomorus*	*Ficus sp.*	*Grewia goetzeana*	*Lannea stuhlmanii*	*Lantana camara*	*Lepisanthes senegalensis*	*Lycopersicon esculentum*	*Manilkara sansibarensis*	*Sideroxylon inerme*	*Sesamum indicum*	*Solanaceae*	*Stadmannia sideroxylon*	*Tamarindus indica*	*Zizyphus mucronata*	Insect
1	V	.03												0.037		0.062										
2	V	11.26		2.157						0.128						0.402						0.047		0.078		0.017
3	V	1.24								0.037			0.013			0.119										
4	V	11.37														1.615					0.026	0.212				0.001
5	B	10.55								0.003						2.062										0.005
6	B	6.89											0.007			0.747										0.001
7	B	12.73											0.005			1.610										0.004
8	B	33.94							0.231							4.134					0.062			0.030		0.024
9	B	25.14											0.007			2.446						0.003				0.002
10	B	8.73														4.422										
11	S	2.27							0.631					0.048												
12	V	1.69								0.194						0.523										0.034
13	V	0.65							0.066							0.200										0.003
14	V	4.80								0.343						0.027								1.075		0.016
15	V	0.45								0.130						0.006										0.003
16	V	9.93		2.296						1.957				0.245		0.065		0.004								0.007
17	V	6.04								0.993						0.018		0.110						2.584		0.004
18	V	2.84								0.886								0.010						0.387		
19	V	1.26								0.352						0.012								0.036		0.007
20	C	1.12																								
21	C	3.61																								
21	C	0.28																								
22	C	0.85																								
23	C	1.61																		0.032						

Table 34 (Continued)

Sample #	Species	Total dry weight - g.	*Azadirachta indica*	*Begonia meyeri-johni*	*Carica papaya*	*Cucumis sativus*	*Elusine sp.*	*Eragrostis sp.*	*Ficus depauperata*	*Ficus exasperata*	*Ficus sonderi*	*Ficus sycomorus*	*Ficus sp.*	*Grewia goetzeana*	*Lannea stuhlmannii*	*Lantana camara*	*Lepisanthes senegalensis*	*Lycopersicon esculentum*	*Manilkara sansibarensis*	*Sideroxylon inerme*	*Sesamum indicum*	*Solanaceae*	*Stadmannia sideroxylon*	*Tamarindus indica*	*Ziziphus mucronata*	Insect
24	C	3.15																								
25	C	1.68								0.001			0.038							0.041						0.003
26	C	0.55																								
27	C	1.74																		0.205				0.012		
28	C	1.63																		0.084						
29	C	3.79																		0.305				0.011		0.004
30	V	1.74		0.245						0.247														0.020		
31	V	1.80								0.068																0.002
32	V	2.83								0.504						0.036				0.034		0.005		0.004		0.005
33	V	1.86							0.013															0.011		0.007
34	V	2.12							0.344					0.012		0.005						0.001				0.015
35	V	3.98							0.261	0.082			0.009	0.026												0.006
36	V	1.66							0.065				0.005			0.134				0.060						
37	S	0.38																								
38	V	8.09												0.134		0.590										0.011
39	S	1.17																		0.067						
40	V	3.75							0.013					0.055		0.320				0.103						
41	C	4.73																		0.634						
42	C	7.00																		0.793						
43	C	7.30																								
44	C	2.76																		0.494						0.003
45	C	2.26																		0.039						
46	B	21.67														4.694					0.460					0.048
47	B	13.16				0.770	0.001	0.001								1.650					0.018					
48	V	5.52		4.488							0.002					0.005					0.002	0.002				
49	V	1.38														0.009								0.218		
50	V	2.07								0.049			0.002								0.013					
51	V	2.97		1.710										0.030				0.025			0.006					0.001
52	V	1.50																		0.046						
53	V	2.68								0.002																0.013

Table 34 (Continued)

Sample #	Species	Total dry weight - g.	*Azadirachta indica*	*Begonia meyeri-johni*	*Carica papaya*	*Cucumis sativus*	*Elusine sp.*	*Eragrostis sp.*	*Ficus depauperata*	*Ficus exasperata*	*Ficus sonderi*	*Ficus sycomorus*	*Ficus sp.*	*Grewia goetzeana.*	*Lannea stuhlmannii*	*Lantana camara*	*Lepisanthes senegalensis*	*Lycopersicon esculentum*	*Manilkara sansibarensis*	*Sideroxylon inerme*	*Sesamum indicum*	*Solanaceae*	*Stadmania sideroxylon*	*Tamarindus indica*	*Zizyphus mucronata*	Insect
54	C	4.55														0.003		0.026		1.106				0.018		
55	V	0.58										0.010				0.014								2.938		0.003
56	V	5.10																				0.005				0.003
57	V	1.44																						1.330		0.007
58	V	1.61		0.465								0.005				0.009								2.672		
59	V	8.41		2.400								0.003												0.722		
60	V	2.72		1.627												0.084										0.007
61	V	2.52												0.043												0.001
62	V	1.47																						2.342		0.013
63	S	5.28																	0.093					1.206		
64	S	3.82																						0.136		0.007
65	S	1.90																						3.140		
66	S	5.91														0.002								1.775		0.005
67	S	5.11																						2.205		
68	S	3.10																						2.456		
69	S	5.07												0.038										0.165		
70	S	2.59												0.235					0.330	0.032				0.274		0.005
71	S	7.69																		0.016						
72	C	2.25									0.001			0.060										0.150		0.246
73	S	5.14												0.030										0.701		
74	S	3.34																						0.031		
75	S	1.81																								
76	C	4.10																						0.004		0.003
76	C	0.52																						0.038		
77	C	4.39																						0.042		
78	C	3.26																		0.310				0.004		
79	C	2.11								0.012		0.009				1.488										0.005
80	B	4.48											0.002			0.254										
81	B	1.74										0.001				0.934										0.017
82	B	10.82				0.029																				

Table 34 (Continued)

Sample #	Species	Total dry weight - g.	*Azadirachta indica*	*Begonia meyeri-johni*	*Carica papaya*	*Cucumis sativus*	*Elusine sp.*	*Eragrostis sp.*	*Ficus depauperata*	*Ficus exasperata*	*Ficus sonderi*	*Ficus sycomorus*	*Ficus sp.*	*Grewia goetzeana*	*Lannea stuhlmannii*	*Lantana camara*	*Lepisanthes senegalensis*	*Lycopersicon esculentum*	*Manilkara sansibarensis*	*Sideroxylon inerme*	*Sesamum indicum*	*Solanaceae*	*Stadmannia sideroxylon*	*Tamarindus indica*	*Ziziphus mucronata*	Insect
83	B	16.28								0.003						2.332										0.066
84	-	number skipped																								
85	B	9.70														2.953										0.042
86	B	25.57											0.074			5.108		0.074								0.007
87	B	19.92								0.064			0.058			3.210		0.017								0.020
88	C	3.25																						0.050		0.003
89	C	1.87																		0.240				0.027		
90	C	3.04																		0.659				0.003		
91	C	1.46																		0.236						
92	C	2.12																						0.066		
93	C	6.70																								
94	C	8.60																		0.023				0.038		
95	C	2.19																						0.015		
96	V	0.82											0.098													0.112
97	V	0.90							→0.058←											0.010						0.017
98	V	3.73							→0.263←																	0.008
99	S	1.90								0.012						0.186										0.002
100	V	4.99									0.843		0.001				0.002	0.004								0.003
101	V	1.72									0.614															0.012
102	V	2.71							0.003		0.028					0.062										0.002
103	B	15.84														0.043										0.002
104	B	12.25																								
105	V	4.45									0.555															
106	V	1.10									0.304		0.003													
107	V	0.67									0.161															
108	V	1.24									0.094															0.001
109	V	2.51									0.665															0.009
110	V	3.23									0.430															0.001
111	V	0.48								0.003			0.004													0.002
112	V	3.76								0.007			0.045		0.056											

Table 34 (continued)

Sample #	Species	Total dry weight - g.	*Azadirachta indica*	*Begonia meyeri-johni*	*Carica papaya*	*Cucumis sativus*	*Elusine sp.*	*Eragrostis sp.*	*Ficus depauperata*	*Ficus exasperata*	*Ficus sonderi*	*Ficus sycomorus*	*Ficus sp.*	*Grewia goetzeana*	*Lannea stuhlmannii*	*Lantana camara*	*Lepisanthes senegalensis*	*Lycopersicon esculentum*	*Manilkara sansibarensis*	*Sideroxylon inerme*	*Sesamum indicum*	*Solanaceae*	*Stadmannia sideroxylon*	*Tamarindus indica*	*Ziziphus mucronata*	Insect
113	V	1.31								0.001					0.377											0.005
114	V	0.73											0.004													
115	V	0.75							0.009																	
116	S	1.43										0.010												0.032		0.002
117	S	1.28																						0.013		0.003
118	C	2.09																		0.508						
119	S	6.01																		0.010			1.370	0.048		0.012
120	S	1.95								0.013										0.002				0.006		0.005
121	S	2.34																						0.057		0.010
122	S	0.35																						0.006		0.010
123	S	1.19																						0.063		
124	S	1.47											0.002											0.015		0.002
125	S	2.12											0.005											0.058		0.007
126	B	8.62											0.195													0.030
127	C	3.38																								
128	C	1.43																						0.003		
129	C	0.93																								
130	S	1.12								0.002																0.030
131	S	1.99											0.030							0.001				0.030		0.026
132	C	3.12																		0.838				0.001		
133	C	6.42											0.015							1.060				0.070		
134	C	2.44										0.057								0.297				0.006		0.001
135	C	2.76											0.157							0.426				0.011		
136	C	1.65																		0.308						0.001
137	C	2.45																						0.002		
138	C	2.40																						0.038		
139	C	2.09																						0.030		
140	C	2.35																						0.060		
141	B	3.15											0.269													0.005

Table 34 (continued)

Sample #	Species	Total dry weight - g.	*Azadirachta indica*	*Begonia meyeri-johni*	*Carica papaya*	*Cucumis sativus*	*Elusine sp.*	*Eragrostis sp.*	*Ficus depauperata*	*Ficus exasperata*	*Ficus sonderi*	*Ficus sycomorus*	*Ficus sp.*	*Grewia goetzeana*	*Lannea stuhlmannii*	*Lantana camara*	*Lepisanthes senegalensis*	*Lycopersicon esculentum*	*Manilkara sansibarensis*	*Sideroxylon inerme*	*Sesamum indicum*	*Solanaceae*	*Stadmannia sideroxylon*	*Tamarindus indica*	*Ziziphus mucronata*	Insect
142	C	1.53																		0.203				0.019		
143	C	2.85																		0.325				0.043		0.004
144	V	0.80								0.002																
145	V	1.80								0.003																0.021
146	V	3.74								0.054							1.350			0.012						0.003
147	V	0.83																								0.007
148	S	2.16								0.175							0.007									0.004
149	V	6.78	0.803										0.011				3.220									0.031
150	V	0.82								0.010							0.038									
151	V	3.52								0.010							0.032									0.016
152	V	0.55								→0.005←																0.003
153	V	2.25								0.006							0.450			0.006						0.006
154	V	1.87								0.075																0.024
155	V	2.81								1.440							0.336									0.017
156	V	2.28	0.554														0.086									0.008
157	V	1.88								0.001																0.004
158	V	1.79								0.010																0.011
159	S	2.94								0.012														0.003		0.020
160	S	3.64											0.002							0.003				0.011	0.780	0.001
161	S	1.18																						0.023		
162	S	3.42																		0.157				0.010	0.523	
163	S	2.42																		0.032				0.006	0.320	
164	S	2.77																						0.267	0.037	
165	S	2.34																						0.021	0.121	0.006
166	S	2.07											0.002											0.017	0.010	0.003
167	B	27.61					0.003			0.100																0.038

B represents baboons.
C represents colobus.
S represents sykes.
V represents vervets.

minus intrusive material) was used. The means of these percentages were calculated on a sample basis (table 35) and a daily basis (table 36). The daily analysis was considered since it was suspected that samples obtained on the same day from each troop would be quite similar in their insect composition. The two methods, however, produced similar results and the sample basis averages were used here.

An analysis of variance was done to determine if the differences among the species in the wet and dry seasons encompassed in this study were statistically significant. In order to perform this significance test, the ratio of insect weight to total weight (i.e., total weight minus intrusive material weight) was transformed to a logarithmic scale; this had the desirable effect of equalizing the variability among the species. If a sample contained no evident insect material, the weight of the insect remains was recorded as .0002 gms. This was done in order to eliminate a large number of zero values which could adversely affect the results of an analysis of variance test. The value of .0002 gms was chosen since it was difficult to identify and weigh insect material at or below this value.

The analysis was run twice, once combining the material from the two vervet troops to give a composite value for vervets as a species for comparison with the

TABLE 35

Insect: (Total - intr.* residue) calculated on a sample basis for troops by seasons

Troop	Season	N	$\bar{X}$%	$\hat{S}$ $(\bar{X})$%
Baboon	Wet	7	.05	.02
	Dry	14	.20	.04
Sykes	Wet	0	-	-
	Dry	33	.52	.21
B's Vervet	Wet	5	.30	.12
	Dry	33	.40	.08
2F Vervet	Wet	13	.45	.10
	Dry	14	.17	.04

* intrusive.

TABLE 36

Insect: (Total - intr.* residue) calculated on a daily basis for troops by seasons

Troop	Season	N	$\overline{X}$%	$\hat{S}$ ($\overline{X}$)%
Baboon	Wet	3	.03	.01
	Dry	7	.20	.45
Sykes	Wet	0	-	-
	Dry	16	.39	.14
B's Vervet	Wet	4	.25	.11
	Dry	10	.26	.06
2F Vervet	Wet	5	.31	.08
	Dry	5	.10	.04

* intrusive.

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other species, and another analysis was done on a troop level, comparing only those troops found in the main study site (i.e., eliminating the 2F vervet troop).

The analysis on the species level (table 37) indicated that while there was no significant difference in the percentage of insect material viewed individually, there was significant interaction between species and season. This indicates that differences among the species change from season to season so that season and species should be considered jointly. However, when the analysis was done comparing only the three troops at the main study site, no statistically significant differences were found, the interaction effect of above no longer being significant (table 38). When the sample average means were plotted (fig. 27), the interaction was seen to be due mainly to the results from the 2F troop. It is not understood why the ratios for the two vervet troops were so different. One possibility could be that the number of troops (2) was too small to make a statement on vervet behavior in general. Also, the construction at the Jadini Hotel could have been affecting behavior patterns to a large extent. No satisfactory explanation is suggested from the study, however.

A "t" test was done to determine whether the differences for particular troops from season to season were significant. It was found that they were significant for both the baboons

TABLE 37

Analysis of variance - on a sample basis for species and season

Source of variation	D.F.	S.S.	Mean square	F
Species	2	1.36	.68	1.33
Season (given species)	1	0.11	.11	.22
Species x Season (given species, season)	1	3.02	3.02	5.92
Residual	114	58.28	.51	
Total (corrected)	118	62.77		

D.F. represents degrees of freedom.
7.2% = coefficient of determination.

TABLE 38

Analysis of variance - on a sample basis for the troops of the main study site and season. (2F troop not included.)

Source of variation	D.F.	S.S.	Mean square	F
Species	2	1.38	.69	1.28
Season (given species)	1	.83	.83	1.54
Species x Season (given species, season)	1	.91	.91	1.69
Residual	87	46.99	.54	
Total (corrected)	91	50.11		

D.F. represents degrees of freedom.
6.22% = coefficient of determination.

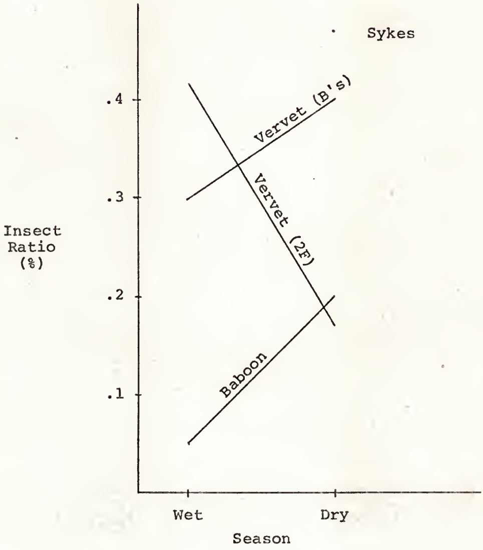

Fig. 27 Plot of interaction on sample basis.

and 2F vervet troop (α = .01, .05, respectively), but not for B's vervet troop. The sykes were used only for dry season comparison since no data was collected from them in the wet season. The R^2 values indicate that only a small portion of the variability in the data was explainable from the variables being tested.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

William R. Maples

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philososphy.

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This dissertation was submitted to the Graduate Faculty of the Department of Anthropology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1974

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